

SYSTEMATIC ANATOMY OF THE XYLEM AND COMMENTS ON THE RELATIONSHIPS OF FLACOURTIACEAE

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SLEUMER (1954) HAS STATED that “. . . no single character exists wherewith to distinguish Flacourtiaceae from other families or to recognize them in the field.” However, the combination of simple generally alternate leaves, numerous stamens, a unilocular ovary with parietal placentation, copious endosperm, and often a glandular receptacle unites this complex of genera into a loosely organized family. This loose organization has resulted in a variety of taxonomic treatments. The wood anatomy of selected Flacourtiaceae has been studied previously, but a comprehensive investigation of the secondary xylem has never been undertaken. Therefore, in an effort to understand more completely the classification of the Flacourtiaceae, this anatomical study, focusing mainly upon tribal and generic relationships, was initiated. Hopefully it will lead to the definition of a more natural taxon. In addition, the validity of previously proposed ordinal and familial alliances is examined to help clarify phylogenetic problems and evolutionary trends. Generic descriptions together with an anatomical circumscription of the family presented in this work will be useful in the identification of unknown wood specimens, in the construction of keys, and in the classification of new taxa.

TAXONOMIC HISTORY

Early taxonomists, such as De Candolle (1824, 1825), Endlicher (1839), and Lindley (1853), treated many of the tribes of the modern Flacourtiaceae as separate “orders,” which are equivalent to the modern rank of family. Gradually the genera of these families (orders) and other genera were united by taxonomists such as Clos (1855, 1857) and Bentham and Hooker (1862, 1867) until the all-inclusive Bixaceae of Baillon (1875) was erected. In 1894 Warburg proposed the segregation of the *Bixa* complex (i.e., those genera usually assigned to the modern concept of Bixaceae and Cochlospermaceae) from the rest of the flacourtiaceous genera. From Warburg to the present this segregation is generally followed. In 1925 Gilg revised Warburg's Flacourtiaceae, suggesting the union of the tribe Erythrospermeae with the tribe Oncobae and proposing the new tribe Trichostephaneae.

In contemporary times three major phylogenetic systems have been proposed. Hutchinson (1967) saw the Flacourtiaceae as the largest and most dominant family in the Bixales, an order of only eight families. Some of Hutchinson's proposed changes within the Flacourtiaceae include the union of Gilg's (1925) tribes Abatieae and Phyllobotryeae with

the tribes Casearieae and Scolopieae, respectively; the exclusion of Gilg's tribe Trichostephaneeae from the Flacourtiaceae; the removal of the tribe Paropsieae to the Passifloraceae; and the removal of the subtribe Prockiinae (tribe Scolopieae) to the Tiliaceae. Hutchinson saw the phyletic position of the Flacourtiaceae as an intermediate group of plants between orders Dilleniales and Tiliales. There seems to be little doubt that Hutchinson pictured the Flacourtiaceae (Bixales) not only as an intermediate group, but also as a primitive group giving rise to orders such as the Thymelaeales, Pittosporales, and Passiflorales.

Cronquist (1968) and Takhtajan (1969) treated the Flacourtiaceae similarly. Takhtajan positioned the family at the base of his Violales, from which he derived the other families in the order. He proposed that members of the Violales were derived from dillenialean forebears and that they were closely related to the Theales. Takhtajan also derived order Passiflorales from the Flacourtiaceae through the Passifloraceae, the basal family of the former order. The tribe Paropsieae, included earlier by some botanists in the Flacourtiaceae, was transferred to the family Passifloraceae.

Cronquist also placed the Flacourtiaceae in order Violales; however, he did not consider the family to be a basal group as did Takhtajan. Cronquist believed that although the Flacourtiaceae was primitive in the order, other families in the Violales did not arise from it directly. In contrast to Takhtajan, Cronquist considered the Violales to be derived from order Theales. He circumscribed the Violales more broadly than Takhtajan and included 20 families to form a somewhat heterogeneous group. Nevertheless, Cronquist stated that these families still belong "to the same general circle of affinity. . . ."

ANATOMICAL REVIEW

Several anatomical studies on segments of Flacourtiaceae have been directed toward clarifying relationships among the genera. In studying the Indonesian Flacourtiaceae Den Berger (1928) noted that the formation of the segregate families Bixaceae and Samydaceae was not consistent with the wood anatomy. He also stated that *Paropsia* differs very strongly from the other genera of Flacourtiaceae, even at first glance. Other pertinent observations made by Den Berger suggest similarities between the Flacourtiaceae and certain Euphorbiaceae, the genus *Siphonodon* (Celastraceae), and the Elaeocarpaceae (Tiliaceae). He also maintained that there is no special link between the Flacourtiaceae and Theaceae. Tupper (1934) concluded that the wood anatomy of Flacourtiaceae was "remarkably and strikingly constant and similar." Taylor (1938) also suggested that the Flacourtiaceae formed a homogeneous unit. Like Den Berger, Taylor concluded that the tribe Paropsieae should be included in the Passifloraceae. In 1964 Ayensu and Stern studied the anatomy of the Passifloraceae and also concluded that the Paropsieae belong in that family.

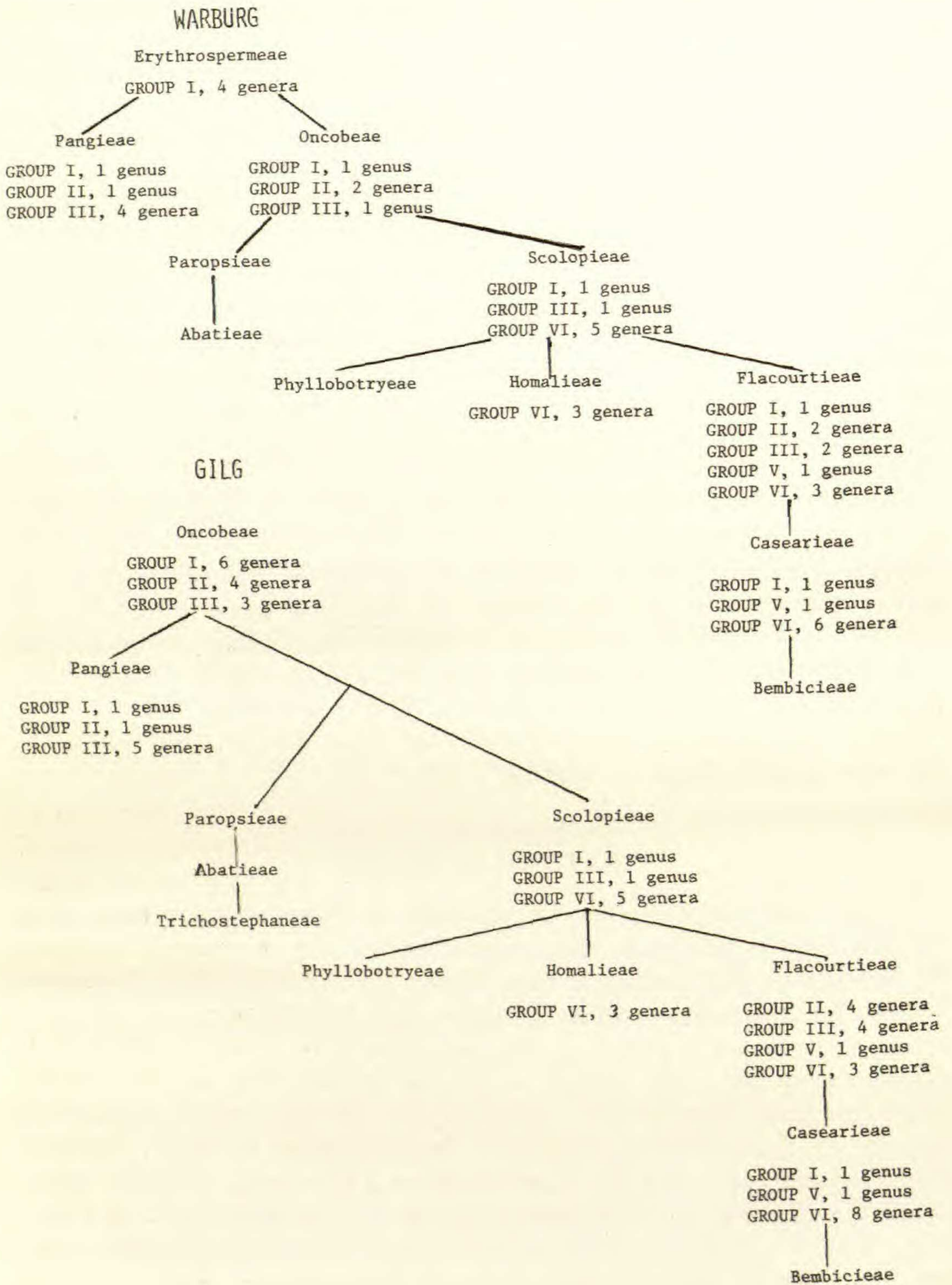


FIGURE 1. The phylogenetic sequences of tribes of Flacourtiaceae as proposed by Warburg (1894) and Gilg (1925). For each tribe the number of genera in each anatomical group is shown.

According to James and Ingle (1956), Flacourtiaceae of the Southwest Pacific area can be divided into two distinct structural groups. One of the groups generally corresponds to Gilg's Oncobeeae and Pangieae, while the other corresponds to Gilg's Scolopieae, Homalieae, Flacourtieae, and Casearieae.

Major anatomical studies of families closely related to Flacourtiaceae include investigations of the Hypericaceae and Guttiferae by Vestal (1937), Dioncophyllaceae and Peridiscaceae by Metcalfe (1952, 1962), Bixaceae by Williams (1962), Cochlospermaceae by Keating (1968), and Violaceae by Taylor (1972). Many of these authors report some degree of relationship with Flacourtiaceae. Pertinent results of these studies will be discussed later.

Other anatomical studies generally have included only descriptions of selected genera or are contained in general reference works. These include studies by Record (1941), Record and Hess (1943), Metcalfe and Chalk (1950), Solereder (1908), Desch (1941), Reyes (1938), Bannan (1943), Miller (1966), and others.

MATERIALS AND METHODS

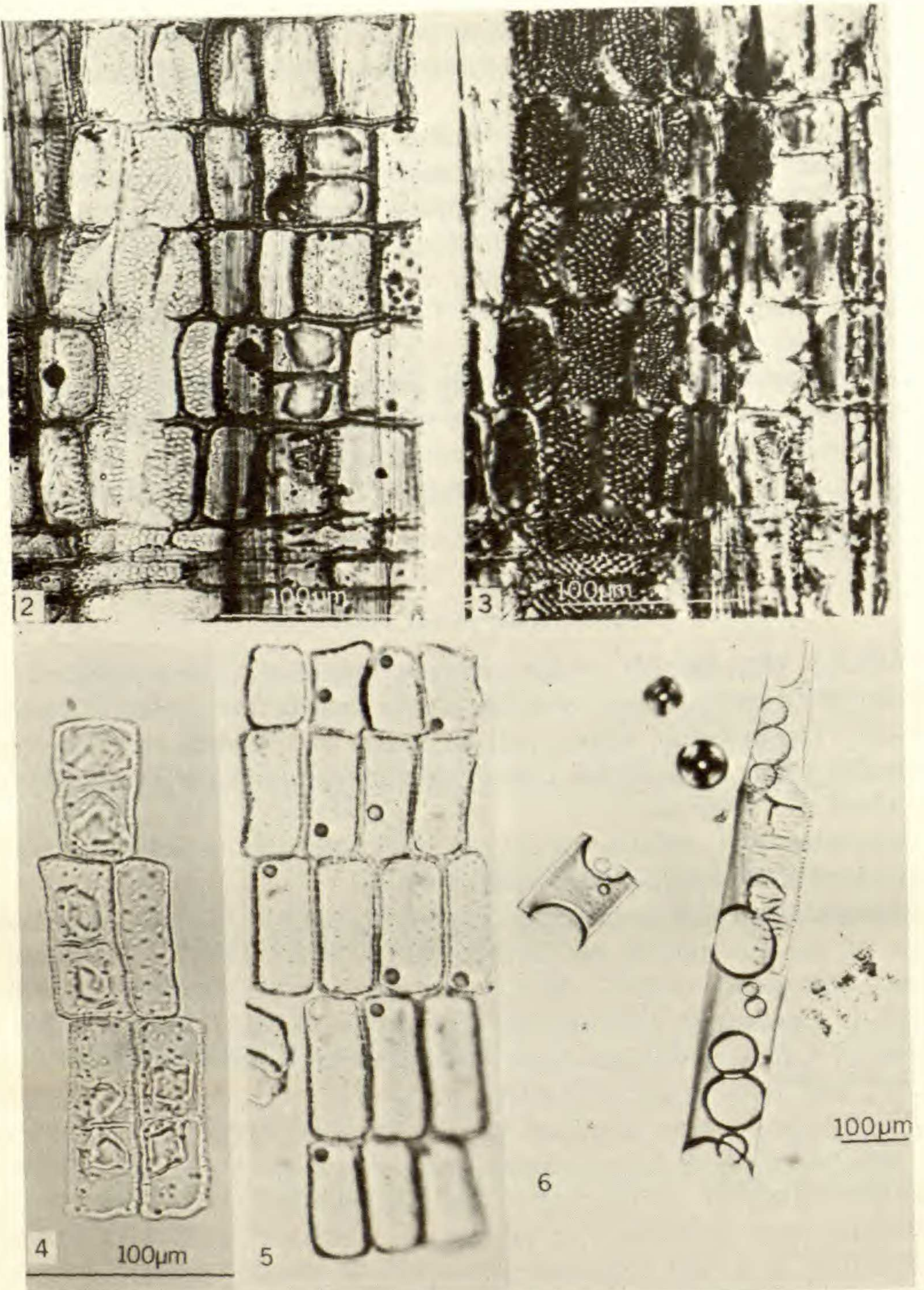
TABLE 1 lists the 241 wood specimens examined. These represent 153 species in 64 genera, approximately 61 per cent of the genera of Flacourtiaceae. The scientific names that accompanied the wood specimens were generally used. Sources for name changes that resulted from synonymy are cited in TABLE 1.

Sectioning and staining techniques were generally standard and have been described fully elsewhere (Miller 1973).

Nomenclature and terminology generally conform to the recommendations of the Committee on Nomenclature, International Association of Wood Anatomists (1957). Standard terms for size classification follow those of Chattaway (1932); the Committee on the Standardization of Terms of Cell Size, International Association of Wood Anatomists (1937, 1939); and Record and Chattaway (1939).

Pore diameters were measured in the tangential direction, and the average was based on 25 measurements. Only the larger pores were included. The percentage of solitary pores and the number of pores per square millimeter were determined by examining an area of "1, 2, 4, or 5 square millimeters, such that it [contained] about 50 to 100 vessels" (Rendle & Clark 1934). In this study, descriptions of radial multiples that exceeded 10 per cent of the total percentage of pores are referred to as "mostly" (e.g., radial multiples mostly 2 and 3). Descriptions of those radial multiples that are less than 10 per cent of the total percentage of pores are referred to as "occasionally" (e.g., occasionally to 5).

Vessel-element lengths were measured from tip to tip. These and fiber (imperforate tracheary elements) lengths are based on 50 measurements. A ratio of the fiber length to vessel-element length (developed by Chattaway, 1936) was computed for each specimen from the average. (This ra-



FIGURES 2-6: 2, radial section of *Calantica cerasifolia* showing prismatic crystals in upright ray cells; 3, same prismatic crystals under polarized light; 4, *Homalium pallidum*, maceration showing the integuments left behind after the prismatic crystals are decomposed; note chambered upright ray cells; 5, *Mayna amazonica*, maceration showing granular type silica in ray cells; 6, dried macerated material of *Hydnocarpus gracilis* treated with concentrated sulfuric acid to show vitreous silica; photographed under polarized light; note birefringence of partially decomposed cells.

ratio is hereinafter referred to as "fiber length to vessel length ratio," F/V.) Chattaway's ratio, which varies from 1.1 to 9.5 in woody dicots, theoretically shows the relative specialization of wood. The closer the value approaches 1.00, the less specialized the wood. This indicates that in primitive species, as a whole, there is little elongation of the cambial derivatives.

The minimum and maximum size of intervacular and vessel-ray pits is reported. Maximum size was determined by measuring the pits in the largest dimension. Where the intervacular and vessel-ray pits are similar in size, the size classification for intervacular pits is given.

Because of the long uniseriate extensions of the heterocellular rays and the vertical fusion of rays, total ray height varied considerably. Consequently, only the multiseriate portion was measured for 25 of the larger rays. The measurements of the 10 largest rays were then averaged. By this method an average ray height for each specimen is obtained which is more easily reproducible and more reliable for comparison and identification purposes than an average obtained by randomly measuring any size ray. The shape and size of ray cells of the multiseriate portion are of diagnostic value. The shape of these individual cells as observed on the radial surface was noted to be elongate, rectangular, or square. The height of individual cells from the multiseriate portion of rays was determined from the tangential section by dividing the number of cells counted over a given distance (at least 150 μm .) into that distance to give an average cell measurement. Only the minimum and maximum values for multiseriate ray-cell height are reported.

The presence of prismatic or druse crystals, presumed to be a form of calcium oxalate (Al-Rais *et al.* 1971; Scurfield, Michell, and Silva 1973), was determined by observing the crystals with polarized light (FIGURE 3). The cell types and the relative abundance in which crystals occurred were recorded for each specimen. In some cases crystals in the upright ray cells are in short chains of two to eight crystals (FIGURES 2, 8, 22). This type of arrangement, in which two to eight crystals in an upright cell are separated from one another by a septum, is called "chambered." An arrangement of two crystals in an upright cell is called two-chambered, three crystals three-chambered, and so forth. Specimens with prismatic crystals that were surrounded by a sheath or integument were also recorded. These integuments can be readily observed, since in macerated preparations the crystal decomposes, leaving the integument as a mold of the crystal (FIGURE 4). When no integuments were found in macerated material and yet crystals were observed in section, a radial free-hand section in which there were at least a few crystals was cut in order to verify the observation. Jeffrey's macerating fluid was then drawn under the cover slip and the crystals were observed with and without polarized light. After 5 to 10 minutes, the crystals completely disappeared and the presence or absence of integuments was determined. When crystals were so infrequent that it could not be determined with

TABLE 1. Wood specimens examined.

SPECIES ^a	COLLECTOR ^b	COLLECTION LOCALITY	HERBARIUM ^c	XYLARIUM ^d
AHERNIA				
<i>glandulosa</i> Merr.	CLPw Mus. Pl. 176	Philippines	None ^e	SJRw ^f 2296
<i>glandulosa</i>	R. Rosenblyth & F. Tamesis <i>s.n.</i>	Philippines	US?	CLPw 11674 ^g
<i>glandulosa</i>	Whitford 73w	Philippines	US?	CLPw 12683 ^g
ANCISTROTHYRSUS				
<i>tessmannii</i> Harms	A. Ducke 290	Brazil	MAD ^h	SJRw 33817
APHLOIA				
<i>myrtiflora</i> Galp.	A. A. Pardy <i>s.n.</i>	S. Rhodesia	None	USw 21257
<i>theiformis</i> (Willd.) Benn.	H. Browne 52-1897	East Africa	None	K-Jw
<i>theiformis</i>	For. Dep.	Mauritius	None	SJRw 15517
<i>theiformis</i>	For. Dep.	Mauritius	None	SJRw 32941
ASTEROPEIA				
<i>micraster</i> Hallier	CTFw 149	Madagascar	None	SJRw 29785
<i>rhopaloides</i> (Baker) Baill.	R. Block 21	Madagascar	None	SJRw 10759
<i>rhopaloides</i>	CTFw 46	Madagascar	None	SJRw 33869
AZARA				
<i>integrifolia</i> R. & P.	D. S. Bullock 70	Chile	None	USw 18895
<i>microphylla</i> Hook. f.	M. Rothkugel & H. Curran 597	Argentina	BAFC?	SJRw 1768
<i>serrata</i> R. & P.	F. G. Meyer 9635	Juan Fernandez Is.	US	USw 34027
<i>serrata</i>		Chile	None	SJRw 34064
<i>uruguayensis</i> (Speg.) Sleum.	W. Herter 1396d	Uruguay	MAD	SJRw 34146
BANARA				
<i>axilliflora</i> Sleum.	Krukoff 5175	Brazil	F	MADw 18988
<i>guianensis</i> Aubl.	B. Maguire & Stahel 22781	Surinam	NY	MADw 11755

<i>guianensis</i>	Ll. Williams 5321	Peru	F	MADw 16421
<i>guianensis</i>	P. Shank 124	Nicaragua	MAD	SJRw 46910
<i>mollis</i> (Poepp. & Endl.) Tul.	Ll. Williams 7031	Peru	F	MADw 23635
<i>nitida</i> Spruce ex Benth.	Ll. Williams 6986	Peru	F	MADw 16424
<i>regia</i> Sandwith	Acosta-Solis 6934	Ecuador	F	MADw 23705
<i>roigii</i> P. Wils.	J. T. Roig 4997; Col. No. 111	Cuba	NY?	SJRw 26541
<i>vellozii</i> Gardn.	H. S. Irwin 2121	Brazil	MAD	SJRw 53071
BARTERIA				
<i>fistulosa</i> Mast.	Breteler 1404	West Africa	WAG	UW 9321
BARTHOLOMAEA				
<i>sessiliflora</i> Steyerf.	Ortiz 109	Guatemala	F	(i)
BENNETTIODENDRON				
<i>leprosipes</i> (Clos) Merr.	SiBoeeca 3788	Sumatra	MICH	USw 28357
<i>leprosipes</i>	Koorders 2085	Java	BZF?	SJRw 30093
BERBERIDOPSIS				
<i>corallina</i> Hook. f.	F. G. Meyer 9766	Chile	US	USw 34057
BUCHNERODENDRON				
<i>speciosum</i> Gürke	Carrington 508	Congo	BR	TERVw ^l 24319
CALANTICA				
<i>cerasifolia</i> Tul.	Thouvenot 74	Madagascar	F	MADw 25421
CALONCOBA				
<i>brevipes</i> (Stapf) Gilg	Cooper 89	Liberia	MAD	USw 4518
<i>brevipes</i>	Cooper 173	Liberia	MAD	USw 4811
<i>brevipes</i>	Cooper 331	Liberia	MAD	SJRw 15237
<i>brevipes</i>	Cooper 470	Liberia	MAD	SJRw 15329
<i>echinata</i> (Oliv.) Gilg	C. Vigne 2804	Ghana	K?	FHOw 8466
<i>echinata</i>	Cooper 122	Liberia	MAD	SJRw 13772
<i>flagelliflora</i> (Mildbr.) Gilg	Devred 1262	Congo	P	(k)
<i>gilgiana</i> (Sprague) Gilg	C. Vigne 2751	Ghana	K?	FHOw 7935

TABLE 1. Wood specimens examined (continued).

SPECIES ^a	COLLECTOR ^b	COLLECTION LOCALITY	HERBARIUM ^c	XYLARIUM ^d
CALONCOBA (con'd)				
<i>glauca</i> (P. Beauv.) Gilg	Escherich 340	Cameroon	B	Bw
<i>glauca</i>	FHI 7718	Nigeria	FHI?	PRFw 23105
<i>schweinfurthii</i> Gilg	Uganda For. Dep. 207; Herb. 1152	Uganda	ENT	FHOw 8245
<i>schweinfurthii</i> Gilg	Uganda For. Dep. 168; Herb. 11	Uganda	ENT	FHOw 13889
<i>welwitschii</i> (Oliv.) Gilg	Sargos 827	Congo	P?	PRFw 15281
<i>welwitschii</i>	Zenker 783	Cameroon	B?	USw 31300
CAMPTOSTYLUS				
<i>aristatus</i> (Oliv.) Gilg	Zenker 1637	Cameroon	B?	Bw
<i>mannii</i> (Oliv.) Gilg	Dechamps 36; wood 522	Congo	BR	TERVw
<i>mannii</i>	Zenker 2860	Cameroon	B?	Bw
CARPOTROCHE				
<i>brasiliensis</i> Endl.	Tatto 35	Brazil	MAD	SJRw 40639
<i>platyptera</i> Pittier	Cooper T. 11	Costa Rica	MAD	SJRw 10473
<i>platyptera</i>	Cooper 377	Panama	MAD	SJRw 11970
<i>platyptera</i>	Terrill 187	Nicaragua	MAD	SJRw 12436
CARRIEREA				
<i>calycina</i> Franch.	Cheng 46	China	?	BWCw 10731
<i>calycina</i>	Chow s.n.	China	None	SJRw 42572
CASEARIA¹				
<i>DASYLEPIS</i> (Sleumer 1972e)				
<i>brevipedicellata</i> Chipp	C. Vigne 2750	Ghana	K	SJRw 23989
DOVYALIS (Sleumer 1972b)				
<i>caffra</i> (Hook. f. & Harv.) Hook. f.	Opdyke 589	Ohio (Cult.)	None	MADw 12235
<i>caffra</i>	Ferreira s.n.	S. Africa	None	USw 20714
ELEUTHERANDRA				
<i>pes-cervi</i> Sloot.	For. Dep. of Java 3499	Indonesia	L?	SJRw 15445
<i>pes-cervi</i>	For. Dep. of Java 4115	Indonesia	L?	SJRw 15446
ERYTHROSPERMUM (Smith 1936)				
<i>acuminatissimum</i> (A. Gray) A. C. Smith	Gillespie 4667	Fiji	BISH	SJRw 25976
<i>acuminatissimum</i>	A. C. Smith 1470	Fiji	MAD	SJRw 28238
<i>candidum</i> (Becc.) Becc.	FPAw 20250	New Guinea	L	USw 24084
FLACOURTIA				
<i>cataphracta</i> Roxb. ex Willd.	W. L. Stern & Wasshausen 2421	Dominica	MAD	USw 35472
<i>indica</i> (Burm. f.) Merr.	A. J. Fors 310	Cuba	SV?	MAD 13915
<i>indica</i>	Schlieben 5464; wood 437	Tanzania	MAD	SJRw 13915
<i>indica</i>	Schlieben 5416; wood 422	Tanzania	MAD	SJRw 33954
<i>rukam</i> Zoll. and Mor.	Krukoff 306	Sumatra	F	USw 31377
<i>rukam</i>	Kanehira 352; wood A1816	Micronesia	FU?	SJRw 20339
<i>rukam</i>	Kanehira 1294; wood A2053	Micronesia	FU?	SJRw 26782
<i>subintegra</i> A. C. Smith	A. C. Smith 1700	Fiji	MAD	SJRw 28328
<i>subintegra</i>	A. C. Smith 1939	Fiji	MAD	SJRw 28426
GOSSYPIOSPERMUM (Wilson 1930)				
<i>praecox</i> (Griseb.) P. Wils.	A. J. Fors 70	Cuba	MAD	MADw 13780
<i>praecox</i>	Rose 8	Venezuela	US	SJRw 2663

TABLE 1. Wood specimens examined (continued).

SPECIES ^a	COLLECTOR ^b	COLLECTION LOCALITY	HERBARIUM ^c	XYLARIUM ^d
GYNOCARDIA				
<i>odorata</i> R. Br.	DD 39643	E. Pakistan	DD	DDw 6177
<i>odorata</i>	G. Gillett 1866	Hawaii (Cult.)	BISH	MADw 25466
HASSETIA				
<i>floribunda</i> H.B.K.	Christopherson 122	Panama	US	MADw 5747
<i>floribunda</i>	Englesing 152	Nicaragua	MAD	SJRw 12427
cf. <i>guatemalensis</i> Warb.	Little 6063	Panama	MAD	MADw 10338
<i>lateriflora</i> Rusby	Espina & Giacometto A116	Colombia	MAD	SJRw 20891
<i>lateriflora</i>	Espina & Giacometto A149	Colombia	MAD	SFRw 20924
<i>laxiflora</i> (Benth.) Eichl.	Ll. Williams 588	Peru	F	MADw 15062
HECATOSTEMON				
<i>guazumaeifolius</i> (H.B.K.) Sleum.	Ll. Williams 9943	Venezuela	F	MADw 23752
HOMALIUM				
<i>foetidum</i> (Roxb.) Benth.	BZFW 6929	Java	?	SJRw 8182
<i>grandiflorum</i> Benth.	For. Dep. of Java 3498	Indonesia	L	SJRw 22357
<i>grandiflorum</i> Benth. var. <i>javanicum</i> (Koord. & Valet.) Sleum.	Koorders 1131c	Java	BZF?	SJRw 30985
<i>guianensis</i> (Aubl.) Warb.	Stahel 372	Surinam	MAD	MADw 19878
<i>hainanense</i> Gagnep.	McClure 18345; wood 11	China	LU?	SJRw 26708
<i>letestui</i> Pellegr.	Cooper 229	Liberia	MAD	SJRw 15155
<i>longifolium</i> Benth.	KEPw 1289; KEP 4784	Malaya	KEP	SJRw 28970
<i>pallidum</i> A. C. Smith	A. C. Smith 1221	Fiji	MAD	SJRw 28136
<i>racemosum</i> Jacq.	Krukoff 6088	Brazil	F	MADw 12297
<i>racemosum</i>	A. J. Fors 1265	Cuba	SV?	MADw 14451
<i>racemosum</i>	RPPRw Tree No. 48	Puerto Rico	RPPR	MADw 17485
<i>smythi</i> Hutch. & Dalz.	Cooper 324	Liberia	MAD	SJRw 15231
<i>smythi</i>	Cooper 469	Liberia	MAD	SJRw 15328
<i>stenophyllum</i> Merr.	Sun Yat Sen U. 70384; wood 834	China	NSM	SJRw 29563
<i>tomentosum</i> (Vent.) Benth.	Col. No. 1890	Burma	DD	SJRw 13178
<i>trichostemon</i> Blake	Ll. Williams 9469	Mexico	MAD	MADw 9877
HYDNOCARPUS (Sleumer 1938)				
<i>gracilis</i> (Sloot.) Sleum.	Krukoff 4164	Sumatra	F	MADw 25423
<i>gracilis</i>	For. Dep. of Java 4308	Indonesia	L?	SJRw 15442
<i>heterophylla</i> Blume	Koorders 1269a	Java	BZF?	SJRw 30098
<i>kunstleri</i> (King) Warb.	For. Dep. of Java 3955	Indonesia	L?	SJRw 22353
<i>kunstleri</i>	KEPw 4033; KEP 46109	Malaya	KEP	SJRw 38716
<i>macrocarpus</i> (Bedd.) Warb.		Burma	None	SJRw 12705
<i>macrocarpus</i>	Col. No. 2913	Burma	DD	SJRw 13111
<i>saigonensis</i> Pierre	Col. No. 3	Burma	DD	SJRw 13182
<i>sumatrana</i> (Miq.) Koord.	CLPw 433	Philippines	CLP	MADw 22588
<i>sumatrana</i>	Koorders 1253c	Java	BZF?	SJRw 30097
<i>venenata</i> Gaertn.	Broadway <i>s.n.</i>	Trinidad	F	SJRw 10940
<i>yatesii</i> Merr.	Krukoff 4165	Sumatra	F	MAD 25422
IDESIA				
<i>polycarpa</i> Maxim.	K. Ogata <i>s.n.</i>	Japan (Cult.)	TOFO	TWTw 155

TABLE 1. Wood specimens examined (continued).

SPECIES ^a	COLLECTOR ^b	COLLECTION LOCALITY	HERBARIUM ^c	XYLARIUM ^d
IDESIA (con'd)				
<i>polycarpa</i>	H. H. Hu 46	China	PE?	SJRw 21462
<i>polycarpa</i>	Fan Mem. Inst. of Biol. 127	China	PE	SJRw 21739
<i>polycarpa</i>	Fan Mem. Inst. of Biol. 377	China	PE	SJRw 21863
ITOA				
<i>stapfi</i> (Koord.) Sleum.	Schram (B. W. 7779)	New Guinea	L	MADw 2569
<i>stapfi</i>	For. Dep. of Java 5425	Indonesia	L	SJRw 15447
KIGGELARIA				
<i>africana</i> L.	PFPw 5410	S. Africa	PRE	SJRw 50377
<i>flavo-velutina</i> Sleum.	Schlieben 3528 (Type); wood 179	Tanzania	MAD	SJRw 27529
LAETIA				
<i>apetala</i> Jacq.	Capucho 466	Brazil	F	MADw 23725
<i>apetala</i>	G. C. Bucher 302	Cuba	NY	SJRw 21437
<i>calophylla</i> Eichl.	Krukoff 7241	Brazil	F	MADw 23669
<i>cupulata</i> Spruce ex Benth.	Ll. Williams 14194	Venezuela	F	MADw 23726
<i>micrantha</i> A. Robyns	Stern <i>et al.</i> 206	Panama	MO	SJRw 54698
<i>micrantha</i>	Stern <i>et al.</i> 513 (Type)	Panama	MO	SJRw 54946
<i>procera</i> (Poepp.) Eichl.	Stahel 124	Surinam	MAD	MADw 19646
<i>procera</i>	Maguire 48294	Brazil	NY	MADw 20267
<i>procera</i>	Maguire 51753	Brazil	NY	MADw 21447
<i>suaveolens</i> (Poepp. & Endl.) Benth.	Ll. Williams 8035	Peru	F	MADw 16436
<i>ternstroemioides</i> Griseb.	Bucher 20	Cuba	NY	SJRw 14737
<i>ternstroemioides</i>	J. G. Jack 5878	Cuba	A	SJRw 16706
<i>thamnia</i> L.	Madera del Trop., Tree No. 49	Yucatán	F	MADw 14988
LETHEDON (= <i>Microsemma</i> Labillardière) (Kostermans 1963)				
<i>le-ratii</i> (Guill.) Kosterm.	McKee 4329	New Caledonia	?	FPAw 14222
<i>setosa</i> (C. T. White) Kosterm.	L. S. Smith 3368	Australia	?	FPAw 11038
LINDACKERIA				
<i>dentata</i> (Oliv.) Gilg	Zenker 879	Cameroon	B?	Bw
<i>dentata</i>	C. Vigne 2468	Ghana	FHO?	SJRw 23251
<i>latifolia</i> Benth.	Ll. Williams 14896	Venezuela	F	MADw 23727
<i>laurina</i> Presl.	H. Pittier 5228	Panama	US	MADw 5778
<i>maynensis</i> Poepp. & Endl.	Krukoff 6159	Brazil	F	MADw 12330
<i>paludosa</i> (Benth.) Gilg	Krukoff 1648	Brazil	F	MADw 23677
<i>paraensis</i> Kuhlman.	A. Ducke 190	Brazil	MAD	SJRw 23652
LUDIA (Sleumer 1972a)				
<i>mauritiana</i> Gmelin	Capuron SF 27114	Madagascar	L	(i)
<i>scolopioides</i> Capuron & Sleum.	M. G. Cours 2768	Madagascar	L	(i)
LUNANIA				
<i>cubensis</i> Turcz.	Bucher 132	Cuba	MAD	SJRw 16841
<i>cubensis</i>	Bucher 257	Cuba	NY	SJRw 21428
<i>parviflora</i> Spruce ex Benth.	Ll. Williams 1895	Peru	F	MADw 15244
<i>parviflora</i>	Krukoff 5275	Brazil	F	MADw 19018
MACROHASSELLTIA (Williams 1961)				
<i>macroterantha</i> (Standl. & L. Wms.) L. Wms.	Barbour 1016	Costa Rica	MAD	MADw 10286
<i>macroterantha</i>	Dayton 3125	Costa Rica	MAD	MADw 10305

TABLE 1. Wood specimens examined (continued).

SPECIES ^a	COLLECTOR ^b	COLLECTION LOCALITY	HERBARIUM ^c	XYLARIUM ^d
MAYNA				
<i>amazonica</i> (Mart.) Macbr.	Krukoff 9001	Brazil	F	MADw 23681
<i>echinata</i> Spruce & Triana	Ll. Williams 4892	Peru	F	MADw 16445
<i>grandifolia</i> (Karst.) Warb.	Dugand, 1014; wood 468	Colombia	MAD	SJRw 33759
<i>longicuspis</i> (Standl.) Standl.	Cooper & Slater 234 (Type)	Panama	MAD	SJRw 10587
<i>longicuspis</i>	Cooper 638	Panama	MAD	SJRw 12271
<i>longifolia</i> Poepp. & Endl.	Ll. Williams 2711	Peru	F	SJRw 17987
<i>odorata</i> Aubl.	Krukoff 4629	Brazil	F	MADw 23685
<i>pacifica</i> Cuatr.	Cuatrecasas 16562	Colombia	US	MADw 23738
<i>zuliana</i> (Pittier) A. Robyns	Stern <i>et al.</i> 908	Panama	MO	SJRw 55120
NEOPTYCHOCARPUS (Buchheim 1959)				
<i>apodanthus</i> (Kuhl.) Buchheim	A. Ducke 416	Brazil	MAD	SJRw 44330
<i>apodanthus</i>	Pires & Silva 11239	Brazil	IAN	IANw
OLMEDIELLA				
<i>betschleriana</i> (Goepp.) Loes.	Salas <i>s.n.</i>	Guatemala	F	SJRw 22081
ONCOBA				
<i>spinosa</i> Forsk.	Schlieben 4133; wood 236	Tanzania	MAD	RBHw 1671
OPHIOBOTRYS				
<i>zenkeri</i> Gilg	Ghana For. Dep. 2056	Ghana	None	SJRw 20025
OSMELIA				
<i>grandistipulata</i> Sloot.	For. Dep. of Java 6285	Indonesia	L?	SJRw 16046
<i>grandistipulata</i>	For. Dep. of Java 6190	Indonesia	L?	SJRw 16047
<i>grandistipulata</i>	For. Dep. of Java 5528	Indonesia	L?	SJRw 16048
<i>philippina</i> (Turcz.) Benth.	SiBoeeca 6752	Sumatra	MICH	USw 28880
<i>philippina</i>	Bartlett 7272	Sumatra	MICH	USw 29390
<i>philippina</i>	Krukoff 4003	Sumatra	F	SJRw 34299
PANGIUM				
<i>edule</i> Reinw.	CLPw 315	Philippines	CLP	MADw 18439
<i>edule</i>	For. Dep. of Java 3315	Indonesia	L?	SJRw 15443
PAROPSIA (Sleumer 1970)				
<i>braunii</i> Gilg	Schlieben 5442; wood 429	Tanzania	MAD	RBHw 1830
<i>guineensis</i> Oliv.	Zenker 727	Cameroon	B?	Bw
<i>madagascariensis</i> (Baill.) Perr.	TEFw 716.R.182	Madagascar	P?	USw 27402
<i>vareciformis</i> (Griff.) Mast.	KEP No. 32695	Malaya	KEP	PRFw 9008
PERIDISCUS				
<i>lucidus</i> Benth.	A. Ducke 113	Brazil	MAD	SJRw 22573
PINEDA				
<i>weberbaueri</i> Irmscher	Iltis & Ugent 539	Peru	WIS	MADw 193
PLEURANTHODENDRON (Williams 1961)				
<i>mexicana</i> (A. Gray) L. Wms.	Ll. Williams 8660	Mexico	F	MADw 9855
<i>mexicana</i>	Ll. Williams 8504	Mexico	MAD	MADw 9869
<i>mexicana</i>	Record G.46	Guatemala	MAD	MADw 10991
<i>mexicana</i>	Kuylen G.59	Guatemala	MAD	MADw 11004
<i>mexicana</i>	Winzerling III.5	Br. Honduras	MAD	MADw 11255
<i>mexicana</i>	Record & Kuylen H.43	Honduras	MAD	SJRw 9989
POLIOTHYRSIS				
<i>sinensis</i> Hook. f.	Kew Gardens	Kew (Cult.)	K	K-Jw

TABLE 1. Wood specimens examined (continued).

SPECIES ^a	COLLECTOR ^b	COLLECTION LOCALITY	HERBARIUM ^c	XYLARIUM ^d
PROCKIA				
<i>crucis</i> P. Br. ex L.	Reitz & Klein 7559	Brazil	WIS	MADw 21831
<i>crucis</i>	H. Pittier 11936	Venezuela	MAD	SJRw 8400
RAWSONIA				
<i>ulugurensis</i> Sleum.	Schlieben 3948; wood 221	East Africa	B	Bw
RYANIA (Monachino 1949)				
<i>angustifolia</i> (Turcz.) Monachino	Froes 12528	Brazil	NY	MADw 21104
<i>angustifolia</i>	Krukoff 7643	Brazil	F	SJRw 34111
<i>angustifolia</i>	Froes 15386	Brazil	NY	SJRw 40678
<i>pyrifera</i> (L. C. Rich.) Uitt. & Sleum.	Krukoff 15402	Trinidad	NY	MADw 21105
<i>speciosa</i> Vahl var. <i>chocoensis</i> (Triana & Planch.) Monachino	Cuatrecasas 15716	Colombia	US	MADw 17541
RYPAROSA				
<i>javanica</i> (Blume) Kurz ex Koord. & Val.	Koorders 30291B; wood 1339c	Java	BZF?	SJRw 30100
<i>kunstleri</i> King	For. Dep. of Java 4167	Indonesia	L?	SJRw 15444
<i>kunstleri</i>	Krukoff 4155	Sumatra	F	SJRw 34374
SAMYDA				
<i>dodecandra</i> Jacq.	G. S. Miller 1676	Puerto Rico	US?	USw 6101
<i>macrantha</i> P. Wils.	J. G. Jack 5893	Cuba	MAD	SJRw 16707
SCAPHOCALYX				
<i>spathacea</i> Ridl.	Selvaraj <i>s.n.</i>	Malaya	KEP	KEPw 11179

SCOLOPIA (Sleumer 1972c)				
<i>luzonensis</i> (Presl.) Warb.	Bartlett 13492	Philippines	MICH	USw 29824
<i>mundii</i> (Nees) Warb.	PFPw 5414	S. Africa	PRE	SJRw 50380
<i>spinosa</i> (Roxb.) Warb.	SiBoeeca 4830	Sumatra	MICH	USw 28616
<i>spinosa</i>	SiBoeeca 5077	Sumatra	MICH	USw 28688
<i>spinosa</i>	For. Dep. of Java 5158	Indonesia	L?	SJRw 22356
<i>spinosa</i>	For. Dep. of Java 5159	Indonesia	L?	SJRw 22888
<i>spinosa</i>	Koorders 2046a	Java	BZF?	SJRw 30086
<i>thouvenotii</i> H. Perrier	Thouvenot 84 (lectotype)	Madagascar	P	MADw 25424
<i>zeyheri</i> (Nees) Harvey	PRFw 5050	S. Africa	PRE?	USw 11945
SCOTTELLIA (Sleumer 1972d)				
<i>klaineana</i> Pierre	Zenker 3018	Cameroon	BR, B	Bw
<i>klaineana</i>	PRFw 7193	Nigeria	FHO?	MADw 16827
<i>klaineana</i>	Cooper 292	Liberia	MAD	SJRw 15204
<i>klaineana</i>	Cooper 369	Liberia	MAD	SJRw 15261
<i>klaineana</i>	Cooper 420	Liberia	MAD	SJRw 15284
<i>klaineana</i> Pierre var. <i>mimfiensis</i> (Gilg) Pellegrin	C. Vigne 2502	Ghana	FHO	SJRw 23261
SOYAUXIA (Brenan 1953)				
<i>grandifolia</i> Gilg & Stapf	Cooper 233	Liberia	MAD	USw 4843
STREPTOTHAMNUS				
<i>moorei</i> F. Muell.	Webb & Tracey 10267	Australia	BRI	(m)
TETRATHYLACIUM				
<i>johansenii</i> Standl.	Curran 329	Colombia	MAD	MADw 10684
<i>macrophyllum</i> Poepp.	Ll. Williams 2713	Peru	F	MADw 16447
TRICHADENIA				
<i>philippinensis</i> Merr.	W. H. Wetmore 9	Philippines	US?	MADw 5270
<i>philippinensis</i>	CLPw 10065 ^g	Philippines	US?	SJRw 2298

TABLE 1. Wood specimens examined (continued).

SPECIES ^a	COLLECTOR ^b	COLLECTION LOCALITY	HERBARIUM ^c	XYLARIUM ^d
TRIMERIA <i>tropica</i> Burkill	Schlieben 5072; wood 345	Tanzania	MAD	SJRw 2945
TRIPHYOPHYLLUM (Shaw 1952) <i>peltatum</i> (Hutch. & Dalz.) Shaw	Cooper 303	Liberia	MAD	SJRw 15213
XYLOSMA <i>benthamii</i> Griseb.	Ll. Williams 12509	Venezuela	F	MADw 23696
<i>congestum</i> Merr.	Fan Mem. Inst. of Biol. 283	China	PE	SJRw 20046
<i>flexuosa</i> (H.B.K.) Hemsl.	Madera del Trop., Tree No. 58	Yucatán	F	MADw 15706
<i>flexuosa</i>	Record BH. 38	Br. Honduras	MAD	SJRw 8806
<i>longifolium</i> Clos	Col. No. C3690	Burma	DD?	SJRw 12530
<i>nelsonii</i> Merr.	Kanehira 3630; wood A2259	Mariana Is.	FU?	SJRw 33238
<i>panamensis</i> Turcz.	Cooper 548	Panama	MAD	MADw 23697
<i>pilosum</i> Macbr.	Ll. Williams 4977 (Type)	Peru	F	SJRw 18640
<i>prunifolium</i> Griseb.	R. Espina 49	Colombia	MAD	SJRw 20498
<i>prunifolium</i>	Dugand 233; wood 70	Colombia	MAD	SJRw 22522
<i>salzmanni</i> (Clos) Eichl.	Ll. Williams 4487	Peru	F	MADw 23744
<i>salzmanni</i>	Hoehne 28203; wood 47	Brazil	MAD	SJRw 23792
<i>venosum</i> N. E. Brown	Col. No. 59	Argentina	MAD	SJRw 15015
ZUELANIA <i>guidonia</i> (Sw.) Britt. & Millsp.	H. Pittier 2710 (Type)	Panama	US	MADw 5771
<i>guidonia</i>	Ll. Williams 8777	Mexico	MAD	MADw 9882
<i>guidonia</i>	Ll. Williams 9164	Mexico	MAD	MADw 9883
<i>guidonia</i>	Ll. Williams 8651	Mexico	MAD	MADw 15688
<i>guidonia</i>	J. G. Jack 5659	Cuba	MAD	SJRw 16644

^a Names cited are those that initially accompanied the specimens, except for names based upon recent taxonomic revisions. When there are appropriate generic monographs, author and date follow names of the genera. Authorities for other synonymies are as follows: Blake (1919), Dale and Greenway (1961), Hutchinson (1967), Hutchinson and Dalziel (1954), Kao (1959), Kuhlmann (1928), Macbride (1941), Pellegrin (1952), Robyns (1968), Shultes (1945), Sleumer (1934, 1938, 1950, 1953, 1954), Williams (1961), and Tisserant and Sillans (1954).

^b Usually refers to the collector and his number, but in some cases refers to the catalog number of an institution.

^c Abbreviations follow those recommended by Lanjouw and Stafleu (1964) in the *Index Herbariorum*.

^d Abbreviations follow those recommended by Stern and Chambers (1960) and Stern (1967) in the *Index Xylariorum*.

^e Refers to specimens collected without accompanying herbarium material.

^f SJRw refers to the Samuel J. Record Memorial Wood Collection formerly cited as Yw and formerly at Yale University School of Forestry; now maintained at the U. S. Forest Products Laboratory, Madison, Wisc.

^g Number refers to former Philippine Bureau of Forestry; abbreviated B.F.

^h MAD refers to the herbarium maintained at the U. S. Forest Products Laboratory, Madison, Wisc., which combines the pre-existent U. S. Forest Products Laboratory herbarium with the herbarium formerly at Yale University School of Forestry (Y).

ⁱ Specimen from herbarium sheet.

^j Unofficial abbreviation of Musée Royal de l'Afrique Centrale, Service d'Anatomie des Bois Tropicaux de la Section d'Economie Agricole et Forestière at Tervuren, Belgium.

^k Slide from Dr. P. Baas and Dr. H. Sleumer at Rijksherbarium, Leiden, Netherlands.

^l Genus examined for Master's Thesis (Miller 1966).

^m Specimen obtained through Dr. S. L. Everist, Botanic Museum and Herbarium, Brisbane, Queensland, Australia.

certainty whether integuments were absent, the notation "no integuments observed" is applied.

Silica deposits, which are chemically unconfirmed *in situ*, occur in the form of dark amorphous granules or glassy casts (vitreous silica). The granular type of silica was observed in maceration (FIGURE 5). The vitreous silica was observed by treating dried macerated material with concentrated sulfuric acid. This process removes most cellulosic and lignin material, leaving the silica casts which appear as a glassy replica of the decomposed cell. Confusion between a silica cast and a partly decomposed cell may be dispelled by observation with polarized light. The silica cast is nonbirefringent, whereas the cellulose cell is birefringent (FIGURE 6). Other deposits are not quantified or qualified and are only classified according to color and relative abundance.

ANATOMICAL DESCRIPTIONS

APPENDIX I lists the more important secondary xylem characters for each genus and may be used as a key to the woods of Flacourtiaceae. The genera in APPENDIX I and in the generic descriptions are arranged in accordance with the scheme of Hutchinson (1967). The tribe Prockieae, which is in Hutchinson's Tiliaceae, follows the tribe Casearieae. After the Prockieae, there is a group labeled "Anomalous Genera" which includes many taxa previously incorporated in Flacourtiaceae.

FAMILY DESCRIPTION

The secondary xylem of Flacourtiaceae is somewhat variable, yet some characters are common to most genera. The wood is diffuse porous with poorly defined to rarely distinct growth rings. Pores are generally rounded or circular in cross-sectional outline, but in *Azara*, *Bennettiodendron*, *Berberidopsis*, *Buchnerodendron*, *Camptostylus*, *Carpotroche*, *Erythrospermum*, *Hydnocarpus*, *Idesia*, *Mayna*, *Osmelia*, *Ryania*, and *Scaphocalyx* the pores are angular. The overall average pore diameter (i.e. the average of individual specimen averages) varies from 34 μm . in *Neoptychocarpus* to 212 μm . in *Streptothamnus*; however, pore diameters are mostly moderately small (50–100 μm .). Generally pores are 50–80 per cent solitary. *Berberidopsis* and *Streptothamnus* have pores that are essentially 100 per cent solitary. Radial multiples consist mostly of two to four pores. Although the overall average number of pores per square millimeter varies from 6 in *Pangium* to over 100 in some species of *Azara*, in most genera the overall average number of pores per square millimeter is numerous to very numerous (20 to over 40) (FIGURES 11, 12, 13).

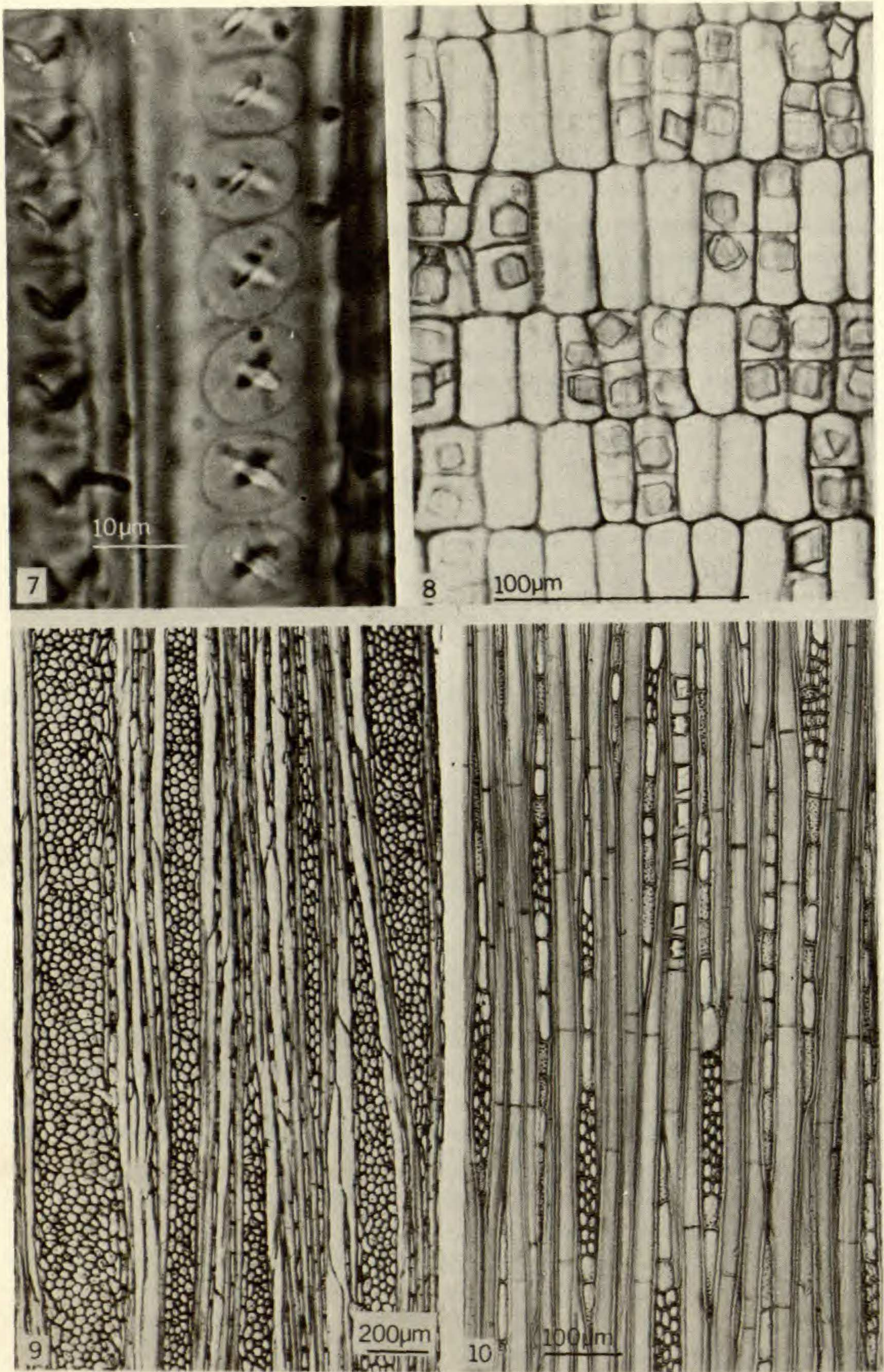
Vessel elements are usually ligulate and vessel walls are 1–8 μm . thick. The overall average length of vessel elements varies from 478 μm . in *Poliothyrsis* to 1794 μm . in *Hydnocarpus*. Spiral thickenings occur throughout the vessels in all species of *Berberidopsis*, *Kiggelaria*, *Olmediella*, *Poliothyrsis*, and *Carrierea* (FIGURE 18). Also, some species of

Mayna, *Scolopia*, *Bennettiodendron*, *Flacourtia*, *Azara*, *Ludia*, *Xylosma*, and *Macrohasseltia* have spirals throughout their vessels. Species with spirals only in the vessel-element tails (ligules) occur in the following genera: *Camptostylus*, *Scottellia*, *Mayna*, *Lindackeria*, *Scolopia*, *Banara*, *Hydnocarpus*, *Bennettiodendron*, *Flacourtia*, *Hasseltia*, *Pleuranthodendron*, and *Macrohasseltia* (FIGURE 14). Tyloses are frequent in species of *Berberidopsis*, *Buchnerodendron*, *Caloncoba*, *Lindackeria*, and *Mayna*. Sclerotic tyloses occur in one specimen of *Eleutherandra*. Perforation plates are exclusively scalariform, simple and scalariform, or exclusively simple in different taxa (FIGURES 15, 16, 17). The end-wall angles are usually oblique. Intervascular pitting is alternate (FIGURES 24, 26), but it is opposite in some species of *Azara*, *Erythrospermum*, *Carpotroche*, *Hydnocarpus*, *Mayna*, and possibly *Neoptychocarpus* (FIGURE 23). The size of the intervascular and vessel-ray pits varies from very small to very large (FIGURES 24–27). Intervascular and vessel-ray pits are frequently unilaterally compound when the pit size is small or very small (FIGURE 27); however, when the pit size is large or very large, unilaterally compound pits are rare.

Rays are of two kinds: uniseriate homocellular rays entirely composed of upright cells and multiseriate heterocellular rays typically with long uniseriate extensions (Heterogeneous Type I, Kribs 1935) (FIGURES 9, 10). Ray height is variable. *Berberidopsis*, *Streptothamnus*, and species of *Casearia* and *Laetia* have rays over 1 cm. in height. On the other hand, some genera have an average ray height of less than 500 μm . Most genera have a ray width of less than 8 cells. Individual cells of the multiseriate portion of the rays as observed on the radial surface are elongate, rectangular, or square. Simply or scalariformly perforated ray cells occur sporadically in a number of genera (FIGURES 19, 20). Axial parenchyma is absent or scanty.

Fibrous elements (= imperforate tracheary elements) are usually septate (FIGURE 10). They are nonseptate in *Berberidopsis*, *Streptothamnus*, and *Idesia*. Both septate and nonseptate fibrous elements occur in *Carreria*, *Itoa*, and *Olmediella*. Pits between fibrous elements are simple and slitlike (libriform wood fibers) or bordered with an extended aperture (fiber-tracheids). *Berberidopsis* and *Streptothamnus* are the only genera in which the fibrous elements are tracheids (FIGURE 7). The shortest fibrous elements occur in *Poliothyrsis* (overall average 874 μm .) and the longest in *Ryparosa* (overall average 3075 μm .). Wall thicknesses of fibrous elements vary from very thin to very thick. The fiber length to vessel length ratio varies from under 1.4 in *Berberidopsis*, *Erythrospermum*, and *Streptothamnus* to 2.4 in *Pangium* and *Trichadenia*.

Prismatic crystals are present in the ray cells of all genera except *Berberidopsis* and *Poliothyrsis*. Prismatic crystals also occur in the fibrous elements of some species of *Banara*, *Homalium*, and *Scolopia* (FIGURE 10). Genera in which prismatic crystals occur in chambered upright ray cells include *Ahernia*, *Banara*, *Bartholomaea*, *Bennettiodendron*, *Camptostylus*, *Calantica*, *Flacourtia*, *Hecatostemon*, *Homalium*, *Lindackeria*,



FIGURES 7-10: 7, radial section of *Streptothamnus moorei* showing bordered pits in tracheids; 8, radial section of *Ahernia glandulosa* showing prismatic crystals in chambered upright ray cells; 9, tangential section of *Ryania angustifolia* showing heterocellular rays typically with long uniseriate extensions (Heterogeneous Type I, Kribs 1935); 10, tangential section of *Banara regia* showing heterocellular rays typically with long uniseriate extensions (Heterogeneous Type I, Kribs 1935) and prismatic crystals in septate fibrous elements.

Ludia, *Oncoba*, *Pineda*, *Scolopia*, *Tetrathylacium*, *Trimeria*, *Hasseltia*, *Macrohasseltia*, *Pleuranthodendron*, and *Prockia* (FIGURES 2, 8, 22). Genera with crystals not encased by an integument include *Buchnerodendron*, *Caloncoba*, *Camptostylus*, *Carpotroche*, *Dasylepis*, *Gynocardia*, *Hydnocarpus*, *Kiggelaria*, *Mayna*, *Osmelia*, *Ryania*, *Ryparosa*, *Scaphocalyx*, and *Streptothamnus*. Druse crystals have been found in some species of *Camptostylus*, *Carrierea*, *Banara*, *Buchnerodendron*, *Laetia*, *Lindackeria*, and *Hasseltia* (FIGURES 21, 22). Granular silica occurs in some species of *Lindackeria*, *Mayna*, and *Scottellia* (FIGURE 5) and vitreous silica occurs in most species of *Hydnocarpus* (FIGURE 6).

GENERIC DESCRIPTIONS

In the generic descriptions numerical measurements which follow pore diameter, vessel-element length, etc. are minimum and maximum individual specimen averages followed by an average of all the specimen averages for a particular genus. When only one specimen of a genus is examined or when no variation in the average exists among a few specimens, the numbers reported are the minimum and maximum individual measurements followed by a specimen average. When variation within a genus is reported, only the species name is cited if an exception applies to all the specimens of a given species. When an exception applies to only part of the specimens of a given species, the xylarium designation and number follow the species cited. The number of species reported for each genus was taken from Willis (1966) and Hutchinson (1967).

Tribe Berberidopsidae

Streptothamnus F. Mueller. Two species endemic in the states of New South Wales and Queensland, Australia. One specimen.

Pore diameter medium-sized to moderately large (176–248 μm .; average 212 μm .); pores 100 per cent solitary; pores per square millimeter moderately numerous (18 pores/ mm^2). Vessel elements very long to extremely long (1159–2745 μm .; average 1976 μm .); perforation plates exclusively scalariform, 6 to 15 bars which are 4–6 μm . thick and 8–14 μm . apart; end-wall angles 10° to 30° . Intervascular pits absent except on overlapping vessel-element ligules; opposite to alternate; medium-sized, 8–10 μm . Vessel-ray pits circular to linear; coarse, 10–40 μm . Height of multiseriate portion of rays mostly over 1.5 cm.; width 3 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 25–37 μm . Tracheids moderately long to extremely long (2074–3416 μm .; average 2644 μm .) with thin to very thin walls, 4–6 μm .; nonseptate. F/V ratio 1.34. Prismatic crystals rare in ray cells of multiseriate portion and absent in upright ray cells; no integuments observed; not in chambered cells.

Berberidopsis Hooker f. Monotypic genus from Chile. One specimen.

Pore diameter moderately small (64–80 μm .; average 72 μm .); pores

99 per cent solitary; pores per square millimeter very numerous (92 pores/mm.²). Vessel elements medium-sized to extremely long (530–2040 μm .; average 1389 μm .); perforation plates exclusively scalariform, mostly over 15 bars which are 2 μm . thick and 4–8 μm . apart, end-wall angles 10° to 25°. Fine spiral thickenings occur throughout the vessel body. Tyloses are occasionally to rarely present. Intervascular pitting very rare or absent except on overlapping vessel-element ligules; opposite; medium-sized to very large, 8–20 μm . Vessel-ray pits circular to linear; coarse, 10–30 μm . Height of multiseriate portion of rays mostly over 1.5 cm.; width 15 to 25 cells or 240–340 μm . Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 20–35 μm . Tracheids medium-sized to moderately long (1550–2200 μm .; average 2644 μm .) with thin walls, 4–6 μm .; nonseptate. F/V ratio 1.37. Crystals absent.

Erythrospermum Lambert. Six to 30 species from Madagascar, Mascarene Islands, Ceylon, India, Burma, Indonesia, and Melanesia. Three specimens representing two species.

Pore diameter moderately small (50–85 μm .; average 62 μm .); pores average 77 per cent solitary, range 69 to 85 per cent; radial multiples mostly 2, occasionally to 4; pores per square millimeter numerous to very numerous (34–61 pores/mm.²; average 52 pores/mm.²). Vessel elements very long (1217–1852 μm .; average 1545 μm .); perforation plates exclusively scalariform, mostly over 15 bars which are 1–3 μm . thick and 4–8 μm . apart; end-wall angles 10° to 15°. Occasional tyloses occur in *E. candidum*. Intervascular pitting opposite to alternate; pits circular to occasionally linear; medium-sized to very large, 7–24 μm . Vessel-ray pits circular to linear; medium to mostly coarse, 8–34 μm . Height of multiseriate portion of rays averages 4753 μm ., range 3645–5581 μm .; width 2 to 6 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 20–50 μm . Simply and scalariformly perforated ray cells in *E. acuminatissimum* (SJRw 25976). Fiber-tracheids moderately long to very long (1786–2344 μm .; average 2110 μm .) with very thin to thick walls, 3–8 μm .; septate. F/V ratio averages 1.38, range 1.27 to 1.47. Prismatic crystals abundant in ray cells of multiseriate portion and abundant to rare in upright ray cells; integumented except in *E. acuminatissimum* (SJRw 25976); not in chambered cells. Reddish-brown deposits frequent in ray cells.

Camptostylus Gilg. Four species from west tropical Africa. Three specimens representing two species.

Pore diameter mostly moderately small (57–105 μm .; average 77 μm .); pores average 79 per cent solitary, range 70 to 91 per cent; radial multiples mostly 2, occasionally to 4; pores per square millimeter numerous to very numerous (31–77 pores/mm.²; average 53 pores/mm.²). Vessel elements moderately long to very long (982–1453 μm .; average 1193 μm .); perforation plates mostly simple to occasionally scalariform, up to 10

bars which are 2 μm . thick and 4–6 μm . apart; end-wall angles 25° to 35°. Spiral thickenings occur in vessel tails of *C. mannii* (TERVw). Intervascular pitting alternate; pits circular to occasionally linear; mostly medium-sized, 8–10 μm .; in *C. mannii* (TERVw) occasionally very large, up to 46 μm . Vessel-ray pits circular to linear; medium to mostly coarse, 8–36 μm . Height of multiseriate portion of rays averages 1308 μm ., range 1075–1660 μm .; width mostly 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 16–35 μm . Fiber-tracheids and libriform fibers moderately long to very long (1877–2532 μm .; average 2128 μm .) with mostly thin walls, 3–6 μm .; septate. F/V ratio averages 1.79, range 1.72–1.91. Prismatic crystals rare to abundant in ray cells of multiseriate portion and absent to frequent in upright ray cells; not integumented; not in chambered cells. Druse crystals in 2- to 4-chambered upright ray cells of *C. mannii* (TERVw). Brown or dark reddish-brown deposits occasionally in ray cells.

Ahernia Merrill. Monotypic genus from Hainan Island and the Philippines. Three specimens.

Pore diameter medium-sized (100–160 μm .; average 123 μm .); pores average 37 per cent solitary, range 29 to 46 per cent; radial multiples mostly 2, occasionally to 5; pores per square millimeter moderately numerous (14–16 pores/mm.²; average 15 pores/mm.²). Vessel elements moderately long (880–1052 μm .; average 980 μm .); perforation plates exclusively simple; end walls somewhat oblique, 30° to 40°. Intervascular pitting alternate; pits circular to oval; medium-sized, 8–10 μm . Vessel-ray pits circular to linear; medium to mostly coarse, 8–30 μm . Height of multiseriate portion of rays averages 897 μm ., range 534–1383 μm .; width 2 to 6 cells. Individual ray cells of multiseriate portion as observed on the radial surface are elongate to rectangular; cell height 15–27 μm . Fiber-tracheids moderately long (1684–1909 μm .; average 1739 μm .) with thin walls, 3–6 μm .; septate. F/V ratio averages 1.84, range 1.81–1.91. Prismatic crystals abundant in upright ray cells and usually absent in ray cells of multiseriate portion; integumented; mostly in 2-, occasionally in 4-chambered upright ray cells.

Dasylepis Oliver. Seven to 10 species from tropical Africa. One specimen.

Pore diameter moderately small (56–80 μm .; average 67 μm .); pores average 84 per cent solitary; radial multiples mostly 2; pores per square millimeter numerous (38 pores/mm.²). Vessel elements moderately long to very long (915–1556 μm .; average 1331 μm .); perforation plates exclusively scalariform, mostly 6 to 13 bars which are 4 μm . thick and 10–14 μm . apart; end-wall angles 10° to 20°. Intervascular pitting alternate; pits circular to linear; medium-sized to very large, 8–20 μm . Vessel-ray pits circular to linear; coarse, 10–22 μm . Height of multiseriate portion of rays averages 2250 μm ., maximum 2850 μm ., width 4 to 6 cells. Indi-

vidual ray cells of multiseriate portion as observed on the radial surface are square to rectangular; cell height 20–27 μm . Fiber-tracheids medium-sized to very long, mostly moderately long (1434–2592 μm .; average 2053 μm .) with thick to very thick walls, 5–8 μm ., septate. F/V ratio 1.54. Prismatic crystals abundant in ray cells of multiseriate portion and rare in upright ray cells; not integumented; not in chambered cells.

Scottellia Oliver. Eight to 10 species from tropical Africa. Six specimens representing one species.

Pore diameter mostly moderately small (66–103 μm .; average 83 μm .); pores average 63 per cent solitary, range 47 to 78 per cent; radial multiples mostly 2, occasionally to 5; pores per square millimeter numerous to very numerous (33–59 pores/mm.²; average 42 pores/mm.²). Vessel elements moderately long to very long (1046–1582 μm .; average 1348 μm .); perforation plates exclusively scalariform, mostly 5 to 15 bars which are 2–6 μm . thick and 8–18 μm . apart; end-wall angles 15° to 30°. Spiral thickenings occasionally in vessel tails; absent in *S. klaineana* (Bw). Intervascular pitting mostly alternate; pits circular to linear; medium-sized to very large, 8–26 μm . Vessel-ray pits circular to linear; medium to mostly coarse, 8–30 μm . Height of multiseriate portion of rays averages 2346 μm ., range 1548–3148 μm .; width 3 to 7 cells. Individual ray cells of the multiseriate portion as observed on the radial surface are square to elongate; cell height 20–30 μm . Fiber-tracheids moderately long to very long (1850–2483 μm .; average 2191 μm .) with thin to thick walls, 3–8 μm .; septate. F/V ratio averages 1.64, range 1.46–1.79. Prismatic crystals frequent to abundant in both types of ray cells, in *S. klaineana* (Bw) rare in ray cells of multiseriate portion and absent in upright ray cells; integumented; not in chambered cells. Very small silica bodies, mostly 6 μm . or less, are rare to frequent in ray cells of multiseriate portion of *S. klaineana*.

Rawsonia Harvey & Sonder. Seven to eight species from tropical Africa and South Africa. One specimen.

Pore diameter moderately small (56–80 μm .; average 68 μm .); pores average 50 per cent solitary; radial multiples mostly 2, occasionally to 6; pores per square millimeter very numerous (83 pores/mm.²). Vessel elements medium-sized to mostly moderately long (589–1140 μm .; average 889 μm .); perforation plates exclusively scalariform, mostly 4 to 10 bars which are 2–4 μm . thick and 10–14 μm . apart; end-wall angles 15° to 30°. Intervascular pitting alternate; pits circular to linear; mostly large to very large, 9–26 μm . Vessel-ray pits circular to linear; medium to mostly coarse, 8–25 μm . Height of multiseriate portion of rays averages 4429 μm ., maximum 6100 μm .; width up to 12 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 15–24 μm . Fiber-tracheids medium-sized to moderately long (1220–1860 μm .; average 1474 μm .) with thin to thick walls, 3–5 μm .; septate. F/V ratio 1.73. Prismatic crystals occasional in ray cells of

multiseriate portion and rare in upright ray cells; integumented; not in chambered cells. Reddish-brown deposits abundant in ray cells.

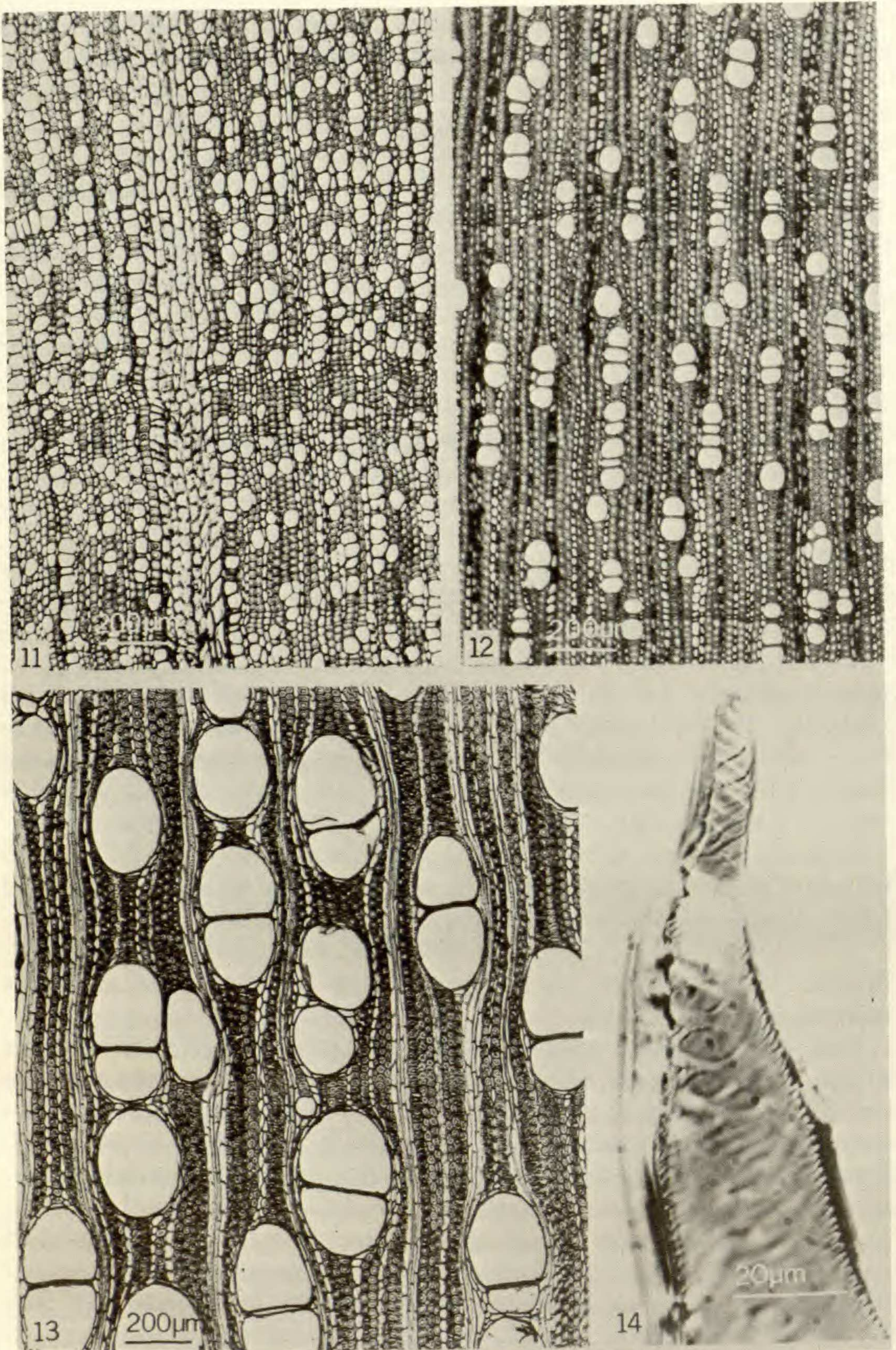
Tribe Oncobeeae

Carpotroche Endlicher. Fifteen to 20 species from Central America and tropical South America. Four specimens representing two species.

Pore diameter very small (42–49 μm .; average 44 μm .); pores average 72 per cent solitary, range 66 to 77 per cent; radial multiples mostly 2, occasionally to 7; pores per square millimeter numerous to very numerous (36–98 pores/mm.²; average 79 pores/mm.²). Vessel elements moderately long (920–1030 μm .; average 993 μm .); perforation plates in *C. platyptera* are exclusively scalariform with 7 to 15 or more bars which are 1–3 μm . thick and 3–8 μm . apart; in *C. brasiliensis* perforation plates are mostly simple and occasionally scalariform (up to 5 bars); end-wall angles 20° to 35°. Occasional tyloses in *C. platyptera* (SJRw 10473 and SJRW 11970). Intervascular pitting mostly alternate to occasionally opposite; pits circular to linear; mostly medium-sized to very large, 7–36 μm . Vessel-ray pits circular to linear; medium to coarse, 8–30 μm . Height of multiseriate portion of rays averages 2363 μm ., range 1979–2653 μm .; width 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to rectangular; cell height 23–50 μm . Simply perforated ray cells in *C. brasiliensis*. Mostly fiber-tracheids, occasionally libriform fibers, medium-sized to moderately long (1387–1889 μm .; average 1535 μm .) with mostly thin to very thin walls, 3–5 μm .; septate. F/V ratio averages 1.55, range 1.38–1.84. Prismatic crystals abundant to occasional in ray cells of multiseriate portion and abundant to rare in upright ray cells; not integumented; not in chambered cells. Reddish-brown deposits frequent to sporadic in ray cells.

Mayna Aublet. Fifteen species from tropical America. Nine specimens representing eight species.

Pore diameter very small to moderately small (38–69 μm .; average 47 μm .); pores average 69 per cent solitary, range 39 to 85 per cent; radial multiples mostly 2, occasionally to 9; pores per square millimeter numerous to very numerous (28–87 pores/mm.²; average 65 pores/mm.²). Vessel elements mostly moderately long to very long (774–1319 μm .; average 974 μm .); perforation plates in *M. longifolia* and *M. pacifica* are exclusively scalariform with 7 to 15 or more bars which are 2–4 μm . thick and 4–10 μm . apart; perforation plates are mostly simple and occasionally scalariform (up to 4 bars) in *M. amazonica*, *M. echinata*, *M. longicuspis* (SJRw 10587), and *M. zuliana*; perforation plates are exclusively simple in *M. grandifolia*, *M. longicuspis* (SJRw 12271), and *M. odorata*; end-wall angles 15° to 55°. Occasional tyloses occur in *M. amazonica*, *M. echinata*, *M. grandifolia*, *M. longicuspis* (SJRw 12271), and *M. zuliana*. Fine spiral thickenings occur throughout the vessel elements of *M. amazonica* and in vessel tails of *M. zuliana*. Intervascular pitting mostly alternate to occasion-



FIGURES 11-14: 11, transverse section of *Ryania angustifolia* showing poorly defined growth rings, little or no axial parenchyma, angular pores, very numerous pores per square millimeter, and an average pore diameter of less than $50\ \mu\text{m}$.; 12 *Lindackeria latifolia*, typical transverse section of Flacourtiaceae with poorly defined growth rings, little or no axial parenchyma, rounded pores,

ally opposite; pits circular to linear; medium-sized to very large, 7–34 μm . Vessel-ray pits circular to linear; medium to coarse, 8–26 μm . Height of multiseriate portion of rays averages 3622 μm ., range 2535–4307 μm .; width 3 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 20–40 μm . Simply perforated ray cells in *M. amazonica*, *M. echinata*, *M. longicuspis* (SJRw 10587), *M. pacifica*, and *M. zuliana*. Fiber-tracheids and libriform fibers medium-sized to moderately long (1263–1990 μm .; average 1517 μm .) usually with thin to very thin walls, 2–6 μm ., thick to very thick, 5–8 μm ., in *M. amazonica*; septate. F/V ratio averages 1.56, range 1.51–1.66. Prismatic crystals abundant to occasional in ray cells of multiseriate portion and frequent to rare in upright ray cells; absent in *M. amazonica*; not integumented; not in chambered cells. Large silica bodies (10–16 μm .) abundant in ray cells of *M. amazonica*. Reddish-brown deposits abundant to occasional in ray cells and fibrous elements.

Oncoba Forskäll. Five to 40 species from tropical Africa and South Africa. One specimen.

Pore diameter mostly moderately small (72–104 μm .; average 85 μm .); pores average 49 per cent solitary; radial multiples mostly 2 and 3, occasionally to 5; pores per square millimeter numerous (31 pores/mm.²). Vessel elements medium-sized to moderately long (518–1128 μm .; average 855 μm .); perforation plates exclusively simple; end-wall angles 30° to 45°. Intervascular pitting alternate; pits circular to oval; medium-sized, 7–8 μm . Vessel-ray pits circular to linear; fine to coarse, 6–25 μm . Height of multiseriate portion of rays averages 345 μm .; maximum 416 μm .; width mostly 2 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 13–16 μm . Simply perforated ray cells present. Fiber-tracheids medium-sized to moderately long (1159–1800 μm .; average 1435 μm .) with mostly thin walls, 4–6 μm .; septate. F/V ratio 1.68. Prismatic crystals frequent in upright ray cells and absent in ray cells of multiseriate portion; integumented; mostly in 2-, occasionally in 4-chambered upright ray cells. Reddish-brown deposits occasional in ray cells.

Caloncoba Gilg. Fifteen to 20 species from tropical Africa. Thirteen specimens representing seven species.

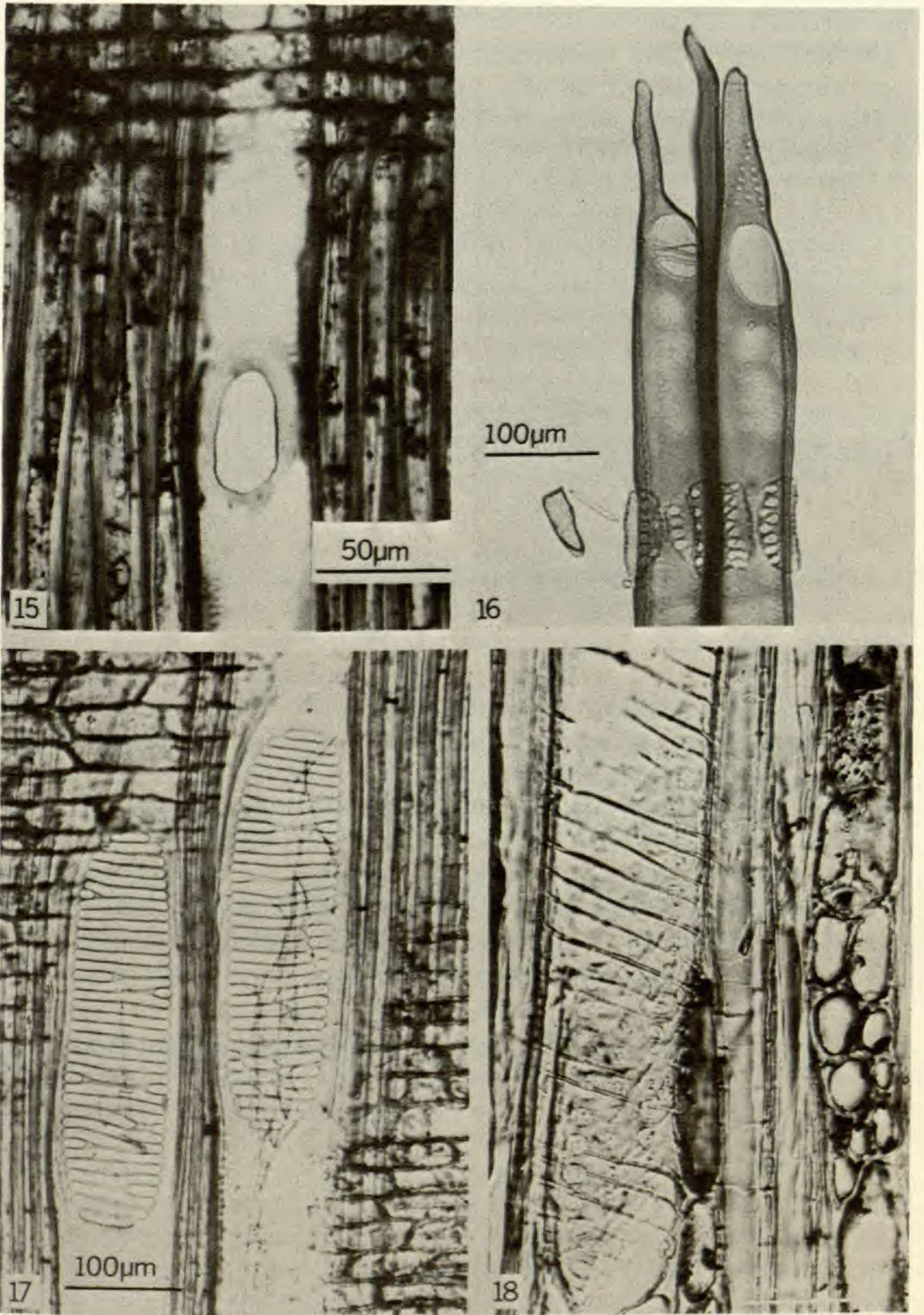
Pore diameter moderately small to medium-sized (52–122 μm .; average 90 μm .); pores average 61 per cent solitary, range 47 to 84 per cent; radial multiples mostly 2, occasionally to 5; pores per square millimeter

numerous pores per square millimeter, and an average pore diameter of 78 μm .; 13, transverse section of *Laetia procera* showing no growth rings, little or no axial parenchyma, rounded pores, moderately few pores per square millimeter, and an average pore diameter of more than 200 μm .; 14, *Pleuranthodendron mexicana*, maceration showing spiral thickenings in the vessel-element tails (ligules); photographed under partially crossed nicols.

moderately numerous to very numerous (11–85 pores/mm.²; average 29 pores/mm.²). Vessel elements mostly moderately long to very long (797–1269 μm .; average 1056 μm .); perforation plates mostly simple and occasionally scalariform with 1 to 10 bars which are 1–4 μm . thick and 4–14 μm . apart; end-wall angles 30° to 45°. Intervascular pitting alternate; pits circular to oval; mostly medium-sized, 8–10 μm . Vessel-ray pits circular to linear; mostly coarse, 10–36 μm . Height of multiseriate portion of rays averages 1387 μm ., range 941–3065 μm .; width mostly 2 to 3 cells, but 3 to 5 cells in *C. echinata* (FHOw 8466) and *C. glauca* (PRFw 23105) and 4 to 7 cells in *C. welwitschii* (PRFw 15281). Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; elongate in *C. flagelliflora*; cell height 23–40 μm . Simply and scalariformly perforated ray cells are usually present; absent in *C. brevipes* and *C. welwitschii* (PRFw 15281). Fiber-tracheids and libriform fibers moderately long to very long (1692–2655 μm .; average 2174 μm .) with very thin to very thick walls, 3–9 μm . F/V ratio averages 2.07, range 1.60–2.30. Prismatic crystals generally more abundant in ray cells of multiseriate portion than in upright ray cells; not integumented; not in chambered cells. Reddish-brown or yellowish deposits abundant to absent in ray cells and fibrous elements.

Lindackeria Presl. Eighteen to 25 species from tropical America and tropical Africa. Seven specimens representing six species.

Pore diameter moderately small (54–89 μm .; average 71 μm .); pores average 49 per cent solitary, range 36 to 61 per cent; radial multiples mostly 2 and 3, occasionally to 9; pores per square millimeter numerous to very numerous (20–47 pores/mm.²; average 33 pores/mm.²). Vessel elements medium-sized to mostly moderately long (705–1182 μm .; average 940 μm .); perforation plates exclusively simple; in *L. dentata* (Bw) perforation plates are mostly simply and rarely scalariform (up to 3 bars); end-wall angles 30° to 50°. Tyloses are occasionally present in all specimens of *Lindackeria* except *L. dentata* (Bw), in which tyloses are absent. Fine spiral thickenings occasionally occur in vessel tails of *L. dentata* (Bw). Intervascular pitting alternate; pits circular to oval; mostly medium-sized, 6–10 μm . Vessel-ray pits circular to linear; medium to coarse, 7–32 μm . Height of multiseriate portion of rays averages 2106 μm ., range 1621–3183 μm .; width 2 to 7 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 20–40 μm . Simply perforated ray cells in *L. maynensis*. Fiber-tracheids and libriform fibers medium-sized to moderately long (1297–1990 μm .; average 1588 μm .) with thin to thick walls, 3–8 μm .; septate. F/V ratio averages 1.70, range 1.42–1.84. Prismatic crystals abundant to rare in ray cells of multiseriate portion and mostly rare to absent in upright ray cells; integumented; not in chambered cells. In *L. dentata* (Bw) druse crystals occasionally occur in 2-, 3-, or 4-chambered ray cells. Silica bodies abundant in both types of ray cells of *L. laurina*. Reddish-brown deposits abundant to occasional in ray cells and fibrous elements.



FIGURES 15-18: 15, radial section of *Buchnerodendron speciosum* showing a simple perforation plate; 16, *Olmediella betschleriana*, maceration showing simple and scalariform perforation plates; note spiral thickenings in vessel element; 17, radial section of *Erythrospermum candidum* showing scalariform perforation plates with many bars; 18, tangential section of *Carrierea calycina* showing spiral thickenings in vessel element.

Buchnerodendron Gürke. Five or six species from tropical Africa. One specimen.

Pore diameter mostly moderately small (48–64 μm .; average 57 μm .); pores average 66 per cent solitary; radial multiples mostly 2, occasionally to 11; pores per square millimeter very numerous (57 pores/ mm^2). Vessel elements medium-sized to mostly moderately long (629–1199 μm .; average 942 μm .); perforation plates mostly simple and occasionally scalariform (up to 5 bars); end-wall angles 20° to 40° . Tyloses occasionally present. Intervascular pitting alternate; pits circular to polygonal; medium-sized, 8–9 μm . Vessel-ray pits circular to linear; medium to coarse, 8–13 μm . Height of multiseriate portion of rays averages 1632 μm ., maximum 2160 μm .; width 3 to 6 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 25–35 μm . Simply and scalariformly perforated ray cells common. Fiber-tracheids medium-sized to moderately long (1081–1945 μm .; average 1536 μm .) with very thin to thin walls, 3–4 μm .; septate. F/V ratio averages 1.63. Prismatic crystals frequent to occasional in ray cells of multiseriate portion and in upright ray cells; not integumented; not in chambered cells. Druse crystals present in ray cells of suspected wounded area.

Tribe Scolopieae

Scolopia Schreber. Forty-five to 55 species from the Old World tropics and subtropics. Nine specimens representing five species.

Pore diameter mostly moderately small (54–105 μm .; average 76 μm .); pores average 59 per cent solitary, range 47 to 71 per cent; radial multiples mostly 2, occasionally to 6; pores per square millimeter numerous to very numerous (20–44 pores/ mm^2 ; average 31 pores/ mm^2). Vessel elements medium-sized to very long (617–1279 μm .; average 881 μm .); perforation plates exclusively simple except in *S. zeyheri*, which has perforation plates that are mostly simple and rarely scalariform; end-wall angles 20° to 45° . Spiral thickenings generally present in the vessel tails; occasional to rare throughout the vessel elements; absent in *S. zeyheri*. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; small, 4–6 μm . Height of multiseriate portion of rays averages 476 μm ., range 226–722 μm .; width 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are elongate; cell height 12–23 μm . Simply perforated ray cells occur in *S. luzonensis*, *S. zeyheri*, and *S. spinosa* (SJRw 22356 and SJRw 30086). Libriform fibers medium-sized to moderately long (1278–2090 μm .; average 1582 μm .) with thin to very thick walls, 3–8 μm .; septate. F/V ratio averages 1.84, range 1.62–2.10. Prismatic crystals abundant in upright ray cells and rare to absent in ray cells of multiseriate portion; in *S. zeyheri* crystals are occasional in both types of ray cells; integumented; mostly in 2- to 4-chambered upright ray cells, occasionally in 6- to 8-chambered cells. Prismatic crystals occasionally in the fibrous elements of *S. spinosa* (USw 28688).

Dark reddish-brown deposits abundant in the ray cells and occasionally in the fibrous elements.

Bartholomaea Standley & Steyermark. Two species from Central America. One specimen from a herbarium sheet.

Pore structure not examined since the twig specimen was very small. Vessel elements medium-sized to moderately long (580–1037 μm .; average 785 μm .); perforation plates mostly simple and rarely scalariform, up to 5 bars which are 2 μm . thick and 4 μm . apart; end-wall angles 20° to 35°. Intervascular and vessel-ray pitting alternate; pits circular, small, 4–6 μm . Rays uniseriate to biseriate; individual ray cells of multiseriate portion as observed on the radial surface are mostly square. Fiber-tracheids medium-sized (946–1403 μm .; average 1144 μm .); septate. F/V ratio 1.46. Prismatic crystals frequent to abundant in both types of ray cells; integumented; mostly in 2- or 4-chambered upright ray cells.

Tribe Banareae

Banara Aublet. Thirty-five to 50 species from the West Indies and Central America to southern Brazil and Paraguay. Nine specimens representing seven species.

Pore diameter very small to medium-sized (42–139 μm .; average 93 μm .); pores average 46 per cent solitary, range 11 to 65 per cent; radial multiples mostly 2 and 3, occasionally to 9; pores per square millimeter moderately numerous to very numerous (14–97 pores/mm.²; average 37 pores/mm.²). Vessel elements medium-sized to moderately long (553–1026 μm .; average 766 μm .); perforation plates exclusively simple; end-wall angles 25° to 60°. Spiral thickenings are rare to occasional in the vessel tails of *B. guianensis* (MADw 11755), *B. roigii*, and *B. vellozii*. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; small, 4–7 μm .; in *B. axilliflora* very small, 2–4 μm . Height of the multiseriate portion of rays averages 276 μm ., range 199–349 μm .; width 2 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 10–23 μm . Fiber-tracheids and libriform fibers medium-sized to moderately long (1025–2000 μm .; average 1414 μm .) with thin to very thick walls, 2–8 μm .; septate. F/V ratio averages 1.84, range 1.47–2.15. Prismatic crystals abundant to rare in upright ray cells, usually absent or rare in ray cells of multiseriate portion; integumented; mostly in 2- to occasionally 4-chambered upright ray cells; in *B. nitida* and *B. roigii* the cells are mostly 4- to 8-chambered. Druse crystals occasionally in upright ray cells of *B. mollis* and *B. regia*. Prismatic crystals occasionally in the fibrous elements of *B. nitida*, *B. regia*, and *B. roigii*.

Pineda Ruiz & Pavon. One to two species from Peru. One specimen.

Pore diameter very small to moderately small (40–56 μm .; average 45 μm .); pores average 49 per cent solitary; radial multiples mostly 2 and

3, occasionally to 10; pores per square millimeter very numerous (86 pores/mm.²). Vessel elements medium-sized to moderately long (400–1102 μm .; average 659 μm .); perforation plates exclusively simple; end-wall angles 20° to 45°. Intervascular pitting alternate; pits circular or oval to polygonal; small to mostly medium-sized, 6–9 μm . Vessel-ray pits mostly circular to oval, occasionally oblong to linear; fine to coarse, 6–20 μm . Height of multiseriate portion of rays averages 223 μm . or 10 cells, maximum 320 μm . or 16 cells; width 2 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to rectangular; cell height 18–23 μm . Simply perforated ray cells present. Fiber-tracheids medium-sized (932–1498 μm .; average 1203 μm .) with thin to thick walls, 3–6 μm .; septate. F/V ratio averages 1.83. Prismatic crystals abundant in upright ray cells and occasional in ray cells of multiseriate portion; integumented; mostly in 2- to occasionally 4-chambered upright ray cells.

Trimeria Harvey. Five to eight species from tropical and South Africa. One specimen.

Pore diameter very small (32–50 μm .; average 39 μm .); pores average 57 per cent solitary; radial multiples mostly 2 and 3, occasionally to 9; pores per square millimeter very numerous (69 pores/mm.²). Vessel elements medium-sized to moderately long (518–1067 μm .; average 816 μm .); perforation plates exclusively simple; end-wall angles 25° to 35°. Intervascular and vessel-ray pitting alternate; pits circular or oval; small to medium-sized, 6–8 μm . Height of multiseriate portion of rays averages 582 μm ., maximum 760 μm .; width 2 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 14–18 μm . Simply perforated ray cells present. Libriform fibers mostly medium-sized (1067–1647 μm .; average 1415 μm .) with thin walls, 4–6 μm .; septate in normal fibers, but nonseptate in gelatinous fibers. F/V ratio averages 1.73. Prismatic crystals abundant in upright ray cells and occasional in ray cells of multiseriate portion; integumented; mostly in 2- to occasionally 4-chambered upright ray cells.

Tribe Homalieae

Calantica Jaubert ex Tul. Five species from tropical East Africa and Madagascar. One specimen.

Pore diameter mostly moderately small (72–104 μm .; average 83 μm .); pores average 42 per cent solitary; radial multiples mostly 2, occasionally to 4; pores per square millimeter moderately numerous (14 pores/mm.²). Vessel elements mostly moderately long to very long (762–1555 μm .; average 1165 μm .); perforation plates exclusively simple; end-wall angles 25° to 35°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; small, 3–5 μm . Height of multiseriate portion of rays averages 452 μm ., maximum 680 μm .; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are rectangular to elongate; cell height 20–30 μm . Fiber-tracheids and libriform

fibers moderately long to very long (1860–2592 $\mu\text{m}.$; average 2245 $\mu\text{m}.$) with very thick walls, 8–11 $\mu\text{m}.$; septate. F/V ratio averages 1.93. Prismatic crystals abundant in upright ray cells and occasional in ray cells of multiseriate portion; integumented; mostly in 2-, occasionally in 3- or 4-chambered upright ray cells. Reddish-brown deposits frequent in ray cells.

Homalium Jacquin. Over 200 species from the tropics and subtropics. Sixteen specimens representing 12 species.

Pore diameter moderately small to medium-sized (77–146 $\mu\text{m}.$; average 97 $\mu\text{m}.$); pores average 45 per cent solitary, range 22 to 80 per cent; radial multiples mostly 2 and 3, occasionally to 7; pores per square millimeter moderately few to numerous (8–38 pores/mm.²; average 22 pores/mm.²). Vessel elements medium-sized to very long (560–1362 $\mu\text{m}.$; average 1056 $\mu\text{m}.$); perforation plates exclusively simple in most species; in *H. longifolium* and *H. pallidum* perforation plates are mostly simple and occasionally scalariform with few or vestigial bars; end-wall angles 15° to 60°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; small, mostly 4–6 $\mu\text{m}.$, occasionally 6–8 $\mu\text{m}.$ Height of multiseriate portion of rays averages 524 $\mu\text{m}.$, range 350–973 $\mu\text{m}.$; width 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are elongate; cell height mostly 13–23 $\mu\text{m}.$; in *H. grandiflorum* cell height 18–27 $\mu\text{m}.$ Fiber-tracheids and libriform fibers medium-sized to moderately long (1115–2247 $\mu\text{m}.$; average 1776 $\mu\text{m}.$) with mostly thick to very thick walls, 4–11 $\mu\text{m}.$; septate. F/V ratio averages 1.70, range 1.27–2.00. Prismatic crystals abundant in upright ray cells, but rare to occasional in *H. stenophyllum*; mostly occasional to absent in ray cells of multiseriate portion, but abundant in *H. longifolium*, *H. pallidum*, and *H. racemosum* (MADw 14451); integumented; mostly in 2- to 4-chambered upright ray cells or cells appearing to be chambered, and frequently more than 1 crystal per chamber; not in chambered cells in *H. letestui*. Prismatic crystals occasionally in scanty paratracheal parenchyma and in the fibrous elements of *H. foetidum*, *H. pallidum*, and *H. racemosum* (MADw 14451). Reddish-brown deposits abundant in the ray cells and fibrous elements of *H. grandiflorum* var. *javanicum*, *H. hainanense*, and *H. trichostemon*; absent in the ray cells of *H. letestui*, *H. smythei*, and *H. tomentosum*; sporadic in the ray cells of the remaining specimens.

Tribe Pangieae

Hydnocarpus Gaertner. Thirty to 40 species from India, Malay Archipelago, and Indo-China. Twelve specimens representing eight species, including the species of *Asteriastigma* and *Taraktogenos*.

Pore diameter moderately small to medium-sized (55–146 $\mu\text{m}.$; average 86 $\mu\text{m}.$); pores average 76 per cent solitary, range 45 to 93 per cent; radial multiples mostly of 2, occasionally to 4; pores per square millimeter moderately numerous to very numerous (13–72 pores/mm.²; average 38 pores/mm.²). Vessel elements very long to extremely long (1296–2361

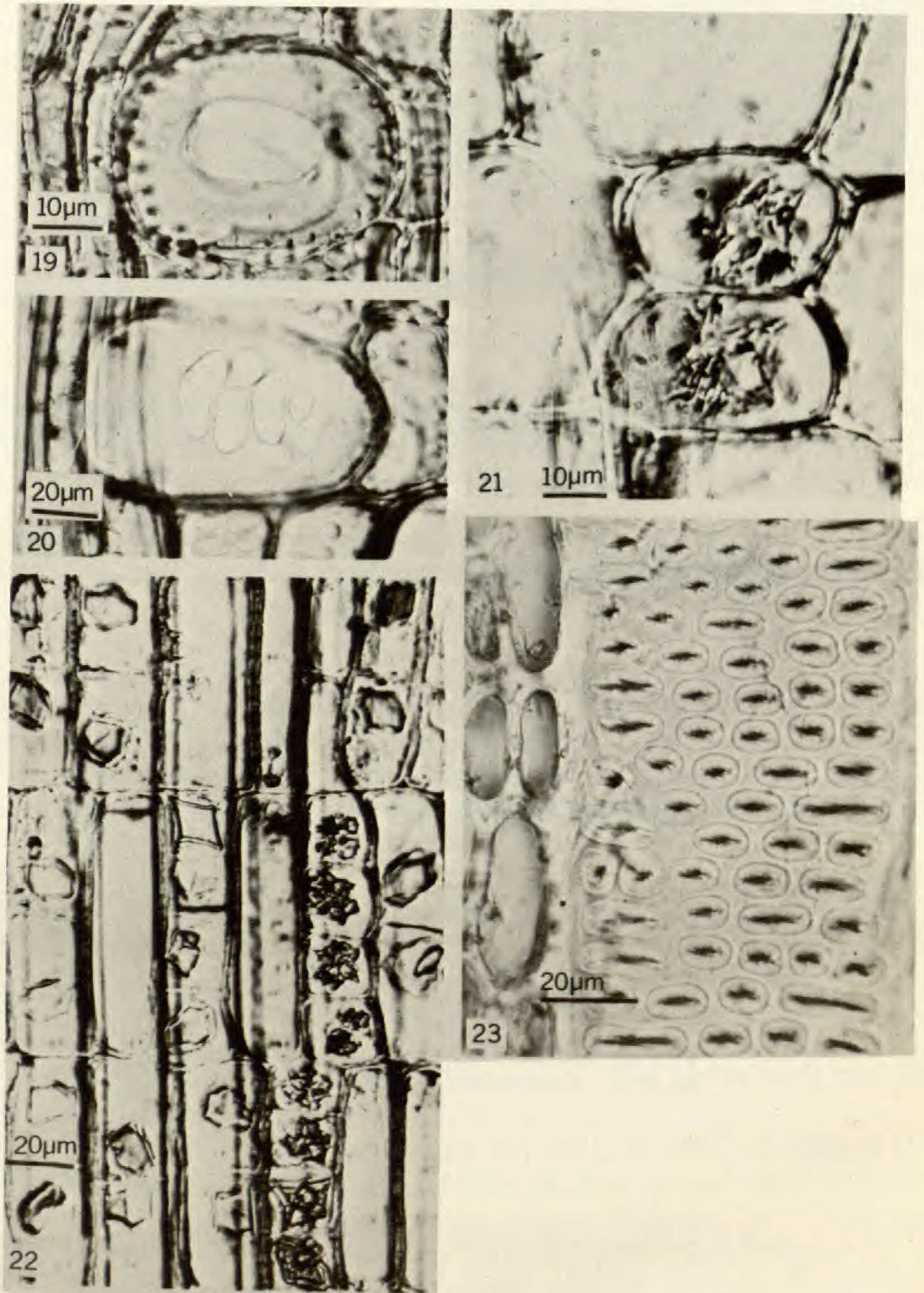
$\mu\text{m.}$; average 1794 $\mu\text{m.}$); perforation plates exclusively scalariform, mostly over 15 bars which are 1–6 $\mu\text{m.}$ thick and 4–16 $\mu\text{m.}$ apart; end-wall angles 10° to 25° . Tyloses occasional to rare in *H. gracilis* (MADw 25423), *H. kunstleri* (SJRw 22353), *H. sumatrana* (MADw 22588), and *H. yatesii*. Spiral thickenings occur in the vessel tails and occasionally throughout vessel elements of *H. kunstleri* (SJRw 38716). Intervascular pitting opposite to alternate; pits circular to oval; medium-sized, mostly 8–10 $\mu\text{m.}$ in *H. gracilis* (MADw 25423), *H. macrocarpus*, *H. sumatrana*, and *H. venenata*; large, mostly 10–14 $\mu\text{m.}$ in the remaining specimens. Vessel-ray pits circular to linear; medium to coarse, 8–44 $\mu\text{m.}$ Height of multiseriate portion of rays averages 1218 $\mu\text{m.}$, range 348–3273 $\mu\text{m.}$; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 23–53 $\mu\text{m.}$ Simply perforated ray cells in *H. kunstleri* (SJRw 38716). Fiber-tracheids moderately long to extremely long (1982–3628 $\mu\text{m.}$; average 2793 $\mu\text{m.}$) with thin to very thick walls, 3–15 $\mu\text{m.}$; septate. F/V ratio averages 1.56, range 1.46–1.81. Prismatic crystals abundant to occasional in both types of ray cells, usually more prevalent in ray cells of multiseriate portion, absent in *H. kunstleri* (SJRw 22353), *H. macrocarpus*, *H. saigonensis*, and *H. yatesii*; not integumented; not in chambered cells. Vitreous silica in the vessel elements and occasionally fibrous elements of all species except *H. sumatrana*. Reddish-brown or brownish-orange deposits in the ray cells of *H. macrocarpus* and *H. sumatrana*.

Eleutherandra Van Slooten. One or two species from Sumatra and Borneo. Two specimens representing one species.

Pore diameter medium-sized (119–126 $\mu\text{m.}$; average 122 $\mu\text{m.}$); pores average 36 per cent solitary, range 24 to 48 per cent; radial multiples mostly 2 and 3, occasionally to 7; pores per square millimeter moderately few (7–8 pores/ mm.^2 ; average 8 pores/ mm.^2). Vessel elements very long (1103–1252 $\mu\text{m.}$; average 1177 $\mu\text{m.}$); perforation plates exclusively simple; end-wall angles 20° to 35° . Sclerotic tyloses occur occasionally in *E. pes-cervi* (SJRw 15445). Intervascular pitting alternate; pits circular to polygonal; small to medium-sized, 6–8 $\mu\text{m.}$ Vessel-ray pits circular to linear; medium to coarse, 8–38 $\mu\text{m.}$ Height of multiseriate portion of rays averages 1640 $\mu\text{m.}$, range 1630–1650 $\mu\text{m.}$; width 1 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 28–40 $\mu\text{m.}$ Fiber-tracheids and occasionally libriform fibers are very long (2306–2736 $\mu\text{m.}$; average 2521 $\mu\text{m.}$) with very thick walls, 10–16 $\mu\text{m.}$; septate. F/V ratio averages 2.13, range 2.09–2.16. Prismatic crystals abundant in both types of ray cells; integumented; not in chambered cells.

Gynocardia R. Brown. Monotypic genus from India and Burma. Two specimens.

Pore diameter moderately small to medium-sized (64–117 $\mu\text{m.}$; average 91 $\mu\text{m.}$); pores average 63 per cent solitary, range 60 to 65 per cent;



FIGURES 19-23: 19, radial section of *Buchnerodendron speciosum* showing simply perforated ray cell; 20, radial section of *Carpotroche brasiliensis* showing modified scalariformly perforated ray cell; 21, radial section of *Laetia procera* showing druse crystals in "paired" upright ray cells; 22, radial section of *Hasseltia floribunda* showing prismatic and druse crystals in chambered upright ray cells; 23, tangential section of *Erythrospermum candidum* showing opposite and transitional intervascular pitting.

radial multiples mostly 2, occasionally to 3; pores per square millimeter moderately numerous (13–19 pores/mm.²; average 16 pores/mm.²). Vessel elements moderately long (1086–1096 μm .; average 1091 μm .); perforation plates mostly simple and occasionally to rarely scalariform with vestigial and few bars, up to 5 bars which are 2 μm . thick and 6 μm . apart; end-wall angles 30° to 45°. Intervascular pitting alternate; pits circular to polygonal; large, 10–14 μm . Vessel-ray pits circular to linear; coarse, 10–40 μm . Height of multiseriate portion of rays averages 560 μm . or 11 cells, maximum 800 μm . or 15 cells; width 1 to 2 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 40–80 μm . Scalariformly perforated ray cells present. Fiber-tracheids moderately long (1782–1934 μm .; average 1858 μm .) with thin to very thin walls, 3–6 μm .; septate. F/V ratio averages 1.70, range 1.64–1.76. Prismatic crystals occasional in either upright ray cells or ray cells of multiseriate portion; no integuments observed; not in chambered cells.

Pangium Reinwardt. One to three species from Malay Archipelago, Philippine Islands, Solomon Islands, and New Guinea. Two specimens representing one species.

Pore diameter medium-sized (139–148 μm .; average 143 μm .); pores average 56 per cent solitary, range 54 to 58 per cent; radial multiples mostly 2, occasionally to 3; pores per square millimeter moderately few (6 pores/mm.²). Vessel elements moderately long (930–1000 μm .; average 965 μm .); perforation plates exclusively simple; end-wall angles 25° to 60°. Intervascular pitting alternate; pits circular to polygonal; medium-sized, 8–10 μm . Vessel-ray pits circular to linear; coarse, 10–56 μm . Height of multiseriate portion of rays averages 2482 μm ., range 1952–3212 μm .; width 3 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 30–50 μm . Fiber-tracheids moderately long to very long (2037–2713 μm .; average 2375 μm .) with thin to thick walls, 5–8 μm .; septate. F/V ratio averages 2.40, range 2.19–2.71. Prismatic crystals abundant to frequent in both types of ray cells; integumented; not in chambered cells.

Trichadenia Thwaites. One to two species from Ceylon, Philippine Islands, New Guinea, and Melanesia. Two specimens representing one species.

Pore diameter medium-sized (149–170 μm .; average 160 μm .); pores average 40 per cent solitary, range 34 to 46 per cent; radial multiples mostly of 2 and 3, occasionally to 4; pores per square millimeter moderately few (8–9 pores/mm.²; average 8 pores/mm.²). Vessel elements very long (1194–1196 μm .; average 1195 μm .); perforation plates exclusively simple; end-wall angles 30° to 50°. Intervascular pitting alternate; pits circular to polygonal; mostly medium-sized, 8–11 μm . Vessel-ray pits circular to linear; mostly coarse, 10–45 μm . Height of multi-

seriate portion of rays averages 2316 $\mu\text{m.}$, range 2006–2625 $\mu\text{m.}$; width 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to rectangular; cell height 26–55 $\mu\text{m.}$ Fiber-tracheids and occasionally libriform fibers are very long to extremely long (2635–3112 $\mu\text{m.}$; average 2874 $\mu\text{m.}$) with thick to very thick walls; 6–15 $\mu\text{m.}$; septate. F/V ratio averages 2.41, range 2.21–2.60. Prismatic crystals abundant to occasional in both types of ray cells; integumented; not in chambered cells.

Scaphocalyx Ridley. Two species from the Malay Peninsula. One specimen.

Pore diameter moderately small (72–88 $\mu\text{m.}$; average 78 $\mu\text{m.}$); pores average 78 per cent solitary, radial multiples mostly 2, occasionally to 4; pores per square millimeter numerous (38 pores/mm.²). Vessel elements moderately long to very long (915–1708 $\mu\text{m.}$; average 1324 $\mu\text{m.}$) perforation plates exclusively simple; end-wall angles 15° to 25°. Intervascular pitting alternate; pits circular to linear; medium-sized to very large, 8–25 $\mu\text{m.}$ Vessel-ray pits circular to linear; medium to coarse, 7–35 $\mu\text{m.}$ Height of multiseriate portion of rays averages 1847 $\mu\text{m.}$, maximum 2299 $\mu\text{m.}$; width mostly 2 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 28–38 $\mu\text{m.}$ Simply perforated ray cells present. Fiber-tracheids and libriform fibers moderately long to very long (1708–2776 $\mu\text{m.}$; average 2385 $\mu\text{m.}$) with mostly thick walls, 6–8 $\mu\text{m.}$; septate. F/V ratio averages 1.80. Prismatic crystals abundant to frequent in ray cells of multiseriate portion and occasional in the upright ray cells; not integumented; not in chambered cells.

Ryparosa Blume. Eighteen to 25 species from Andamans, Indo-China, Malay, and New Guinea. Three specimens representing two species.

Pore diameter medium-sized (108–154 $\mu\text{m.}$; average 130 $\mu\text{m.}$); pores average 58 per cent solitary, range 33 to 74 per cent; radial multiples mostly 2, occasionally to 5; pores per square millimeter moderately few to moderately numerous (7–17 pores/mm.²; average 13 pores/mm.²). Vessel elements very long (1445–1678 $\mu\text{m.}$; average 1592 $\mu\text{m.}$); perforation plates mostly simple and occasionally scalariform with vestigial and up to 15 or more bars which are 1 $\mu\text{m.}$ thick and 2–4 $\mu\text{m.}$ apart; end-wall angles 15° to 25°. Intervascular pitting alternate; pits mostly circular; large, 10–14 $\mu\text{m.}$ Vessel-ray pits circular to linear; coarse, 12–50 $\mu\text{m.}$ Height of multiseriate portion of rays averages 3423 $\mu\text{m.}$, range 1955–4197 $\mu\text{m.}$; width 3 to 8 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square to occasionally elongate; cell height 25–40 $\mu\text{m.}$ Simply perforated ray cells in *R. kunstleri* (SJRw 15444). Fiber-tracheids and libriform fibers very long to extremely long (2762–3246 $\mu\text{m.}$; average 3075 $\mu\text{m.}$) with thick to very thick walls, 7–17 $\mu\text{m.}$; septate. F/V ratio averages 1.93, range 1.91–1.94.

Prismatic crystals frequent to occasional in ray cells of multiseriate portion and occasional to absent in upright ray cells; not integumented; not in chambered cells.

Kiggelaria Linnaeus. One to four species from tropical Africa and South Africa. Two specimens representing two species.

Pore diameter moderately small (72–96 μm .; average 83 μm .); pores average 52 per cent solitary; radial multiples mostly 2 and 3, occasionally to 4; pores per square millimeter numerous (22–37 pores/ mm^2 ; average 30 pores/ mm^2). Vessel elements medium-sized (642–797 μm .; average 720 μm .); perforation plates exclusively simple; end-wall angles 20° to 45°. Spiral thickenings occur throughout the vessel elements. Inter-vascular pitting alternate; pits circular to polygonal; medium-sized, 8–10 μm . Vessel-ray pits circular to linear; medium to coarse, 7–26 μm . Height of multiseriate portion of rays averages 1008 μm ., range 872–1145 μm .; width 3 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 23–35 μm . Fiber-tracheids and libriform fibers medium-sized (1291–1583 μm .; average 1437 μm .) with mostly thin walls, 3–6 μm .; septate. F/V ratio averages 2.00, range 1.99–2.01. Prismatic crystals rare in ray cells of multiseriate portion and absent in upright ray cells; no integuments observed; not in chambered cells.

Tribe Flacourtieae

Olmediella Baillon. Monotypic genus known only in cultivation, generally from Mexico and Honduras. One specimen.

Pore diameter moderately small (64–120 μm .; average 94 μm .); pores average 61 per cent solitary; radial multiples mostly 2 and 3, occasionally to 6; pores per square millimeter numerous (36 pores/ mm^2). Vessel elements moderately long (549–1189 μm .; average 844 μm .); perforation plates mostly simple and rarely scalariform; end-wall angles 20° to 35°. Coarse spiral thickenings common throughout the vessels. Inter-vascular pitting alternate; pits circular to linear; large to very large, 10–34 μm . Vessel-ray pits circular to linear; coarse, 10–32 μm . Height of multiseriate portion of rays averages 1606 μm ., maximum 2161 μm .; width 4 to 6 cells. Individual ray cells of multiseriate portion as observed on the radial surface are very elongate; cell height 20–35 μm . Simply perforated ray cells. Fiber-tracheids and libriform fibers moderately long (1828–1951 μm .; average 1890 μm .) with thin to very thick walls, 4–10 μm .; mostly septate, some nonseptate fibrous elements. F/V ratio 2.23. Prismatic crystals abundant in both types of ray cells; integumented; not in chambered cells; occasionally many small crystals in one cell.

Bennettiodendron Merrill. Three species from India, southern China, and Malay Archipelago. Two specimens representing one species.

Pore diameter mostly moderately small (47–67 μm .; average 58 μm .); pores average 70 per cent solitary; radial multiples mostly 2 and 3, occasionally to 6; pores per square millimeter very numerous (61–94 pores/ mm^2 ; average 76 pores/ mm^2). Vessel elements moderately long (847–1094 μm .; average 970 μm .); perforation plates mostly simple and occasionally to rarely scalariform with up to 5 bars; end-wall angles 10° to 20° . Fine spiral thickenings occasionally throughout the vessel elements or more commonly in vessel tails. Intervascular pitting alternate; pits circular to occasionally linear; mostly medium-sized to large, 8–14 μm .; occasionally very large, up to 25 μm . Vessel-ray pits circular to linear; medium to coarse, 8–25 μm . Height of multiseriate portion of rays averages 308 μm ., range 263–354 μm .; width 2 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 18–30 μm . Fiber-tracheids and libriform fibers medium-sized to moderately long (1092–1780 μm .; average 1436 μm .) with thin walls, 2–4 μm .; septate. F/V ratio averages 1.46, range 1.30–1.63. Prismatic crystals abundant in upright ray cells and occasional in ray cells of multiseriate portion; integumented; mostly in 2-, occasionally in 3- or 4-chambered upright ray cells. Yellowish-brown deposits common in rays.

Flacourtia Commerson ex L'Héritier. Fifteen to 60 species from tropical Africa, Southeast Asia, Malaysia, and Fiji Islands. Nine specimens representing four species.

Pore diameter mostly moderately small (48–77 μm .; average 66 μm .); pores average 41 per cent solitary, range 28 to 66 per cent; radial multiples mostly 2 and 3, occasionally to 7; pores per square millimeter moderately numerous to numerous (17–32 pores/ mm^2 ; average 23 pores/ mm^2). Vessel elements medium-sized to very long (616–1201 μm .; average 876 μm .); perforation plates exclusively simple; however, in *F. subintegra* (SJRw 28328), a few vestigial bars occur; end-wall angles 25° to 55° . Spiral thickenings throughout vessel elements or in the vessel tails of *F. indica* (MADw 13915). Intervascular and vessel-ray pitting alternate; pits circular to polygonal; small, 4–6 μm . Height of multiseriate portion of the rays averages 350 μm ., range 256–408 μm .; width mostly 2 to 3 cells, occasionally 6. Individual ray cells of multiseriate portion as observed on the radial surface are rectangular to elongate; cell height mostly 13–23 μm .; in *F. subintegra* (SJRw 28426) cell height 16–26 μm . Simply perforated ray cells common; absent in *F. indica* (MADw 13915 and SJRW 33954) and *F. rukam* (USw 31377). Fiber-tracheids and libriform fibers medium-sized to moderately long (1018–2194 μm .; average 1545 μm .) with thin to very thick walls, 3–11 μm .; septate. F/V ratio averages 1.78, range 1.60–2.00. Prismatic crystals abundant to occasional in upright ray cells and rare to absent in ray cells of multiseriate portion; in *F. indica* (MADw 13915) and *F. subintegra* crystals are abundant in both types of ray cells; integumented; mostly in 2- to 4-chambered upright ray cells. Reddish-brown deposits common in the rays and fibrous elements.

Dovyalis E. Meyer ex Arnott. Twenty to 30 species from tropical Africa and South Africa, Ceylon, and New Guinea. Two specimens representing one species.

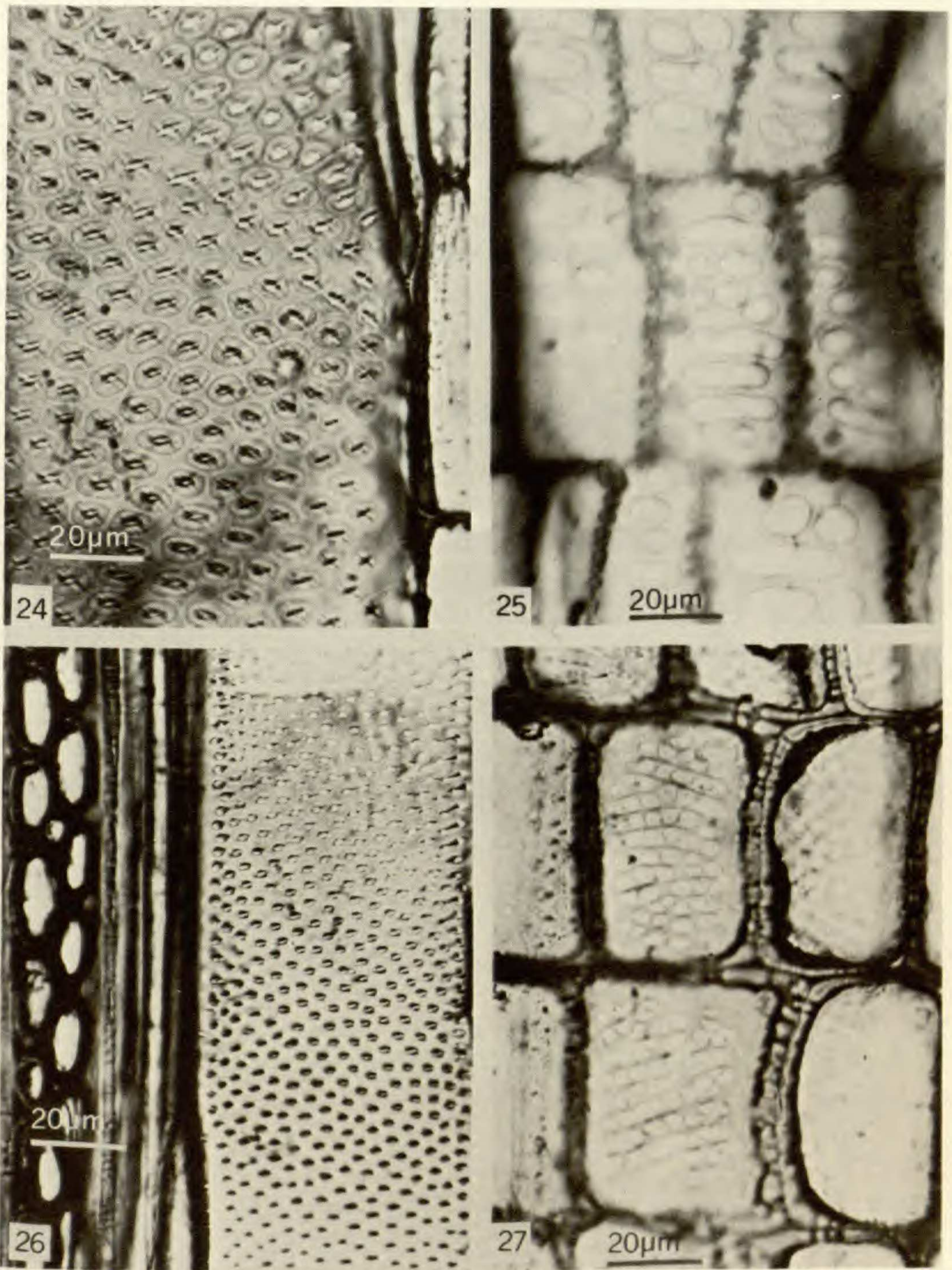
Pore diameter very small (36–49 μm .; average 43 μm .); pores average 63 per cent solitary, range 60 to 65 per cent; radial multiples mostly 2 and 3, occasionally to 6; pores per square millimeter very numerous (46–51 pores/ mm^2 ; average 49 pores/ mm^2). Vessel elements medium-sized (485–508 μm .; average 496 μm .); perforation plates mostly simple and occasionally scalariform with vestigial and up to 8 bars which are 2–3 μm . thick; end-wall angles 15° to 45° . Intervascular and vessel-ray pitting alternate; pits circular to polygonal; small, 4–6 μm . Height of multiseriate portion of the rays averages 373 μm ., range 326–420 μm .; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 15–23 μm . Simply perforated ray cells in *D. caffra* (USw 20714). Fiber-tracheids medium-sized (945–983 μm .; average 964 μm .) with mostly thin walls, 2–4 μm .; septate. F/V ratio averages 1.95, range 1.86–2.03. Prismatic crystals abundant in both types of ray cells; integumented; not in chambered cells.

Azara Ruiz & Pavon. Eleven to 28 species from western Argentina, Chile, and Juan Fernandez Islands. Five specimens representing four species.

Pore diameter very small to moderately small (37–96 μm .; average 58 μm .); pores average 45 per cent solitary, range 28 to 70 per cent; radial multiples mostly 2 and 3, occasionally to 16; pores per square millimeter very numerous (56–121 pores/ mm^2 ; average 83 pores/ mm^2). Vessel elements medium-sized (404–704 μm .; average 526 μm .); perforation plates mostly simple and occasionally scalariform with up to 4 bars; in *A. serrata* (USw 34027) perforation plates are exclusively scalariform with 6 to 15 bars which are 2–3 μm . thick and 4–6 μm . apart; end-wall angles 10° to 30° . Very coarse spiral thickenings common throughout the vessels of *A. microphylla*. Intervascular pitting alternate to occasionally opposite; pits circular to oval; medium-sized to large, 8–12 μm .; in *A. serrata* (USw 34027) intervacular pitting is opposite; pits circular to linear and large to very large, 10–44 μm . Vessel-ray pits circular to linear; medium to coarse, 8–28 μm . Height of multiseriate portion of rays averages 257 μm ., range 229–277 μm .; width 2 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 15–25 μm ., in *A. serrata* (USw 34027) cell height is 20–35 μm . Fiber-tracheids moderately short to medium-sized (687–1029 μm .; average 901 μm .) with thin walls, 2–5 μm .; septate. F/V ratio averages 1.73, range 1.46–1.88. Prismatic crystals frequent to occasional in both types of ray cells; absent in *A. serrata* (USw 34027); integumented; mostly not in chambered cells, occasionally in 2-chambered cells in *A. integrifolia*. Reddish-brown deposits common in rays.

Ludia Commerson ex Jussieu. Six or seven species from East Africa, Madagascar, and Mascarene Islands. Two specimens, both from herbarium sheets, representing two species.

Pore structure not examined since the twig specimens were very small. Vessel elements medium-sized (373–712 μm .; average 543 μm .); per-



FIGURES 24–27: 24, tangential section of *Ahernia glandulosa* showing medium-sized intervacular pits; 25, radial section of *A. glandulosa* showing coarse vessel-ray pits; 26, tangential section of *Calantica cerasifolia* showing small intervacular pits; 27, radial section of *C. cerasifolia* showing fine vessel-ray pits and unilaterally compound pitting.

foration plates mostly simple, occasionally scalariform with a few bars or with vestigial bars; end-wall angles 10° to 45° . Fine spiral thickenings occasionally present throughout the vessels of *L. scolopioides*. Intervascular and vessel-ray pitting alternate; pits circular to oval; small, 4–5 μm . Height of multiseriate portion of rays averages 452 μm ., range 224–680 μm .; width mostly 2 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square; cell height 16–23 μm . Simply and scalariformly perforated ray cells present. Fiber-tracheids moderately short to medium-sized (627–1088 μm .; average 858 μm .) with mostly thin walls, 2–5 μm .; septate. F/V ratio averages 1.61, range 1.53–1.68. Prismatic crystals abundant in upright ray cells, occasional in ray cells of multiseriate portion; integumented; mostly in 2- to 4-chambered upright ray cells.

Xylosma G. Forster. About 100 species from the American and Asian tropics and warm temperate regions, absent in Africa. Thirteen specimens representing 10 species.

Pore diameter very small to medium-sized (37–111 μm .; average 76 μm .); pores average 52 per cent solitary, range 31 to 74 per cent; radial multiples mostly 2 and 3, occasionally to 21; pores per square millimeter moderately numerous to very numerous (17–103 pores/mm.²; average 37 pores/mm.²). Vessel elements medium-sized to moderately long (633–1143 μm .; average 851 μm .); perforation plates exclusively simple; end-wall angles 40° to 50° . Fine spiral thickenings common throughout the vessels of *X. benthamii*, *X. congestum*, *X. flexuosa* (SJRw 8806), *X. longifolium*, *X. pilosum*, *X. salzmanni*, and *X. venosum*. Intervascular pitting alternate; pits circular to polygonal and small, 4–6 μm ., in *X. flexuosa* (SJRw 8806), *X. longifolium*, *X. nelsonii*, *X. panamensis*, *X. pilosum*, and *X. prunifolium*; pits small to medium-sized, 6–8 μm ., in *X. benthamii*, *X. congestum*, *X. flexuosa* (MADw 15706), *X. salzmanni*, and *X. venosum*. Vessel-ray pits circular to oval; similar in size to their respective intervascular pits. Height of multiseriate portion of rays averages 581 μm ., range 318–1270 μm .; width 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate and the cell height is 13–20 μm . in *X. benthamii*, *X. congestum*, *X. longifolium*, *X. pilosum*, *X. prunifolium*, and *X. salzmanni* (MADw 23744); the ray cell type is square to elongate and the cell height is 20–35 μm . in *X. flexuosa*, *X. nelsonii*, *X. panamensis*, *X. salzmanni* (SJRw 23792), and *X. venosum*. Simply perforated ray cells occur in *X. flexuosa* (SJRw 8806), *X. longifolium*, *X. prunifolium* (SJRw 22522) and *X. salzmanni* (SJRw 23792). Fiber-tracheids and libriform fibers medium-sized to moderately long (1128–1802 μm .; average 1457 μm .) with mostly thin to very thin, occasionally thick, walls, 2–6 μm .; septate. F/V ratio averages 1.73, range 1.50–2.37. Prismatic crystals abundant to frequent in upright ray cells, mostly occasional to rare in ray cells of multiseriate portion; in *X. flexuosa* (MADw 15706) crystals are abundant in both types of ray cells; integumented; generally in 2-chambered upright ray cells, not in chambered cells in *X. congestum* and *X. flexuosa* (MADw 15706).

Reddish-brown deposits generally common in rays and fibrous elements; absent in *X. congestum*, *X. panamensis*, and *X. salzmanni* (SJRw 23792).

Poliothyrsis Oliver. One to three species from China and Celebes. One specimen.

Pore diameter very small to moderately small (40–56 μm .; average 46 μm .); pores average 50 per cent solitary; radial multiples mostly 2 and 3, occasionally to 11; pore clusters common; pores per square millimeter very numerous (79 pores/mm.²). Vessel elements moderately short to medium-sized (278–695 μm .; average 478 μm .); perforation plates exclusively simple; end-wall angles 15° to 30°. Fine spiral thickenings frequent throughout vessel. Intervascular pitting alternate; pits circular to oval; medium-sized to large, 8–11 μm . Vessel-ray pits circular to linear; medium to coarse, 8–16 μm . Height of multiseriate portion of rays averages 213 μm . or 14 cells, maximum 227 μm . or 17 cells; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 12–18 μm . Fiber-tracheids moderately short to medium-sized (669–1086 μm .; average 874 μm .) with mostly very thin walls, 2–3 μm .; septate. F/V ratio averages 1.83. Prismatic crystals absent.

Carrierea Franchet. Three or four species from southern and western China and Indo-China. Two specimens representing one species.

Pore diameter moderately small (63–68 μm .; average 66 μm .); pores average 54 per cent solitary, range 51 to 56 per cent; radial multiples mostly 2 and 3, occasionally to 5; pores per square millimeter mostly very numerous (39–49 pores/mm.²; average 44 pores/mm.²). Vessel elements medium-sized (705–730 μm .; average 718 μm .); perforation plates mostly simple and occasionally scalariform with vestigial and up to 3 bars which are 2 μm . thick; end-wall angles 15° to 40°. Very coarse spiral thickenings common throughout the vessel. Intervascular pitting alternate; pits mostly circular, occasionally to linear; mostly large, 10–14 μm .; occasionally very large, up to 16 μm . Vessel-ray pits circular to linear; medium to mostly coarse, 8–20 μm . Height of multiseriate portion of the rays averages 164 μm . or 8.5 cells, range 110 μm . (5 cells) to 217 μm . (12 cells); width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 15–20 μm . Fiber-tracheids and libriform fibers medium-sized (1291–1354 μm .; average 1322 μm .) with mostly very thin walls, 2–3 μm .; only septate in nongelatinous and latewood fibrous elements. F/V ratio averages 1.84, range 1.83–1.84. Prismatic and druse crystals occasional to rare in both types of ray cells; integumented; not in chambered cells, but druse crystals generally occur in “paired” upright ray cells.

Itoa Hemsley. Two species from eastern Asia and New Guinea. Two specimens representing one species.

Pore diameter medium-sized (171–186 μm .; average 178 μm .); pores average 39 per cent solitary, range 30 to 48 per cent; radial multiples

mostly 2, occasionally to 4; pores per square millimeter moderately few (6–8 pores/mm.²; average 7 pores/mm.²). Vessel elements moderately long (847–887 μm .; average 867 μm .); perforation plates exclusively simple; end-wall angles 60° to 80°. Intervascular pitting alternate; pits mostly circular to polygonal; mostly large, 10–15 μm .; occasionally linear and very large (up to 120 μm .) in *I. stapfi* (MADw 2569). Vessel-ray pits circular to linear; coarse, 10–36 μm . Height of multiseriate portion of rays averages 462 μm ., range 454–470 μm .; width 2 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are elongate; cell height 18–23 μm . Fiber-tracheids and libriform fibers moderately long (1770–1836 μm .; average 1803 μm .) with thin to very thin walls, 2–4 μm .; septate in normal wood, but nonseptate in gelatinous fibers. F/V ratio averages 2.08, range 2.07–2.08. Prismatic crystals abundant in upright ray cells, rare or absent in ray cells of multiseriate portion; integumented; not in chambered cells.

Idesia Maximowicz. Monotypic genus from China and Japan. Four specimens.

Pore diameter moderately small (65–82 μm .; average 74 μm .); pores average 55 per cent solitary, range 46 to 61 per cent; radial multiples mostly 2 and 3, occasionally to 8; pores per square millimeter very numerous (44–61 pores/mm.²; average 55 pores/mm.²). Vessel elements medium-sized to moderately long (764–930 μm .; average 870 μm .); perforation plates mostly exclusively simple; in *I. polycarpa* (TWTw 155) mostly simple and rarely scalariform with up to 5 bars which are 2 μm . thick; end-wall angles 15° to 50°. Occasional tyloses in *I. polycarpa* (TWTw 155). Intervascular pitting alternate; pits circular, large, 10–12 μm . Vessel-ray pits circular to oval, medium to coarse, 8–12 μm . Height of multiseriate portion of the rays averages 447 μm ., range 383–543 μm .; width 2 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are elongate; cell height 18–25 μm . Fiber-tracheids medium-sized (1246–1626 μm .; average 1466 μm .) with thin to very thin walls, 2–4 μm .; nonseptate. F/V ratio averages 1.68, range 1.62–1.75. Prismatic crystals frequent to rare in upright ray cells, absent in ray cells of multiseriate portion; completely absent in *I. polycarpa* (SJRw 21863); integumented; not in chambered cells.

Tribe Caseariae

Casearia Jacquin. About 160 to 250 species from both the New and Old World tropics and subtropics. Eighty-six specimens representing 27 species from the New World. Description condensed from unpublished Master's thesis, entitled "Systematic wood anatomy of the American *Casearia* Jacq." (Miller 1966).

Pore diameter mostly moderately small (46–108 μm .; average 75 μm .); pores average 46 per cent solitary, range 22 to 78 per cent; radial multiples mostly 2, occasionally to 6; pores per square millimeter moderately

numerous to very numerous (10–96 pores/mm.²; average 31 pores/mm.²). Vessel elements medium-sized to very long (550–1350 μm .; average 937 μm .); perforation plates exclusively simple; end-wall angles 15° to 70°. Intervascular and vessel-ray pitting alternate, pits circular to polygonal; mostly very small, 2–4 μm .; occasionally 5–6 μm . Height of multiseriate portion of rays variable, approximate range 300–2000 μm . and as high as 3000–7000 μm . in *C. javitensis* and *C. iquitosensis*; width mostly 2 to 3 cells and as wide as 12 cells in *C. javitensis* and *C. iquitosensis*. Individual ray cells of multiseriate portion as observed on the radial surface are square in some species and elongate in others; cell height less than 20 μm . in some species and more than 20 μm . in others. Simply perforated ray cells present in some species. Fiber-tracheids and libriform fibers moderately short to moderately long (882–1960 μm .; average 1444 μm .) with mostly thin to thick walls; septate. F/V ratio averages 1.54. Prismatic crystals common in ray cells of most species, but variable in frequency and location; integumented; not in chambered cells. Reddish-brown deposits common in some species.

Gossypiospermum Urban. Two to three species from Cuba and tropical South America. Two specimens representing one species.

Pore diameter very small (35–48 μm .; average 42 μm .); pores average 53 per cent solitary, range 50 to 56 per cent; radial multiples mostly 2 and 3, occasionally to 7; pores per square millimeter very numerous (70–77 pores/mm.²; average 74 pores/mm.²). Vessel elements medium-sized (546–698 μm .; average 622 μm .); perforation plates exclusively simple; end-wall angles 30° to 50°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; very small, 3–4 μm . Height of multiseriate portion of rays averages 634 μm ., range 451–818 μm .; width mostly 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 11–16 μm . Libriform fibers medium-sized (1031–1097 μm .; average 1064 μm .) with thick to very thick walls, 4–6 μm .; septate. F/V ratio averages 1.73, range 1.57–1.89. Prismatic crystals in *G. praecox* (MADw 13780) abundant in both types of ray cells, in *G. praecox* (SJRw 2663) crystals abundant in upright ray cells and occasionally in ray cells of multiseriate portion; both have integumented crystals and both do not have crystals in chambered cells.

Laetia Loefling ex Linnaeus. Ten to 20 species from West Indies and Mexico to tropical South America. Thirteen specimens representing eight species.

Pore diameter very small to moderately small (45–98 μm .; average 73 μm .); in *L. procera* medium-sized to moderately large (112–217 μm .; average 175 μm .); pores average 50 per cent solitary, range 28 to 84 per cent; radial multiples mostly 2 and 3, occasionally to 9; pores per square millimeter moderately numerous to very numerous (16–92 pores/mm.²; average 40 pores/mm.²); in *L. procera*, mostly moderately few (6–11 pores/mm.²; average 8 pores/mm.²). Vessel elements medium-sized to

very long (729–1400 μm .; average 1007 μm .); perforation plates exclusively simple in all *Laetia* except *L. calophylla*, which has perforation plates that are mostly simple and occasionally scalariform with up to 15 or more bars which are 2 μm . thick and 4 μm . apart; end-wall angles 15° to 65° . Intervascular and vessel-ray pitting alternate; pits circular to polygonal; mostly very small, 2–5 μm .; in *L. calophylla* and *L. procera* small, 5–7 μm . Height of multiseriate portion of rays averages 1771 μm ., range 878–4647 μm .; in *L. cupulata* rays are over 5 cm. high. Ray width 2 to 7 cells; in *L. cupulata* up to 15 cells or 240 μm . Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 16–40 μm .; in *L. micrantha* very elongate and 11–16 μm . in height. Simply perforated ray cells in *L. apetala* (SJRw 21437), *L. calophylla*, *L. micrantha* (SJRw 54698), *L. suaveolens*, and *L. ternstroemioides* (SJRw 16706). Fiber-tracheids and libriform fibers medium-sized to very long (1262–2522 μm .; average 1727 μm .) with mostly thick to very thick walls, 3–14 μm .; septate. F/V ratio averages 1.72, range 1.53–2.09. Prismatic crystals abundant to frequent in both types of ray cells; in *L. micrantha* and *L. procera* crystals frequent in upright ray cells and rare in ray cells of multiseriate portion; crystals absent in *L. calophylla* and *L. cupulata*; integumented and not in chambered cells in all *Laetia*. Stalked and stalkless druse crystals in “paired” upright ray cells of *L. procera* (MADw 19646, MADw 21447). Reddish-brown deposits abundant to frequent in ray cells and occasionally in fibrous elements of *L. cupulata*, *L. micrantha*, and *L. suaveolens*.

Hecatostemon Blake. Monotypic genus from Venezuela. One specimen.

Pore diameter moderately small (56–80 μm .; average 60 μm .); pores average 53 per cent solitary; radial multiples mostly 2, occasionally to 3; pores per square millimeter numerous (25 pores/ mm^2). Vessel elements medium-sized to very long (397–1220 μm .; average 838 μm .); perforation plates exclusively simple; end-wall angles 35° to 45° . Intervascular and vessel-ray pitting alternate; pits circular to polygonal; very small, 3–4 μm . Height of multiseriate portion of rays averages 328 μm ., maximum 368 μm .; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 13–18 μm . Simply perforated ray cells observed. Fiber-tracheids and libriform fibers medium-sized to moderately long (1250–1891 μm .; average 1512 μm .) with mostly thin walls, 3–5 μm .; septate. F/V ratio averages 1.80. Prismatic crystals frequent in upright ray cells and rare in ray cells of multiseriate portion; integumented; rarely in chambered upright ray cells.

Ryania Vahl. Eight to 14 species from northern tropical South America and Trinidad. Five specimens representing three species.

Pore diameter very small to moderately small (39–75 μm .; average 54 μm .); pores average 70 per cent solitary, range 56 to 84 per cent; radial multiples mostly 2, occasionally to 7; pores per square millimeter very

numerous (47–98 pores/mm.²; average 72 pores/mm.²). Vessel elements mostly moderately long (864–1155 μm .; average 987 μm .); perforation plates exclusively simple in *R. pyrifer* and *R. speciosa* var. *chocoensis*; mostly simple and rarely scalariform with vestigial or few bars in *R. angustifolia*; end-wall angles 20° to 40°. Intervascular and vessel-ray pitting alternate; pits circular to oval; small, 4–6 μm . Height of multiseriate portion of rays averages 5878 μm ., range 5157–6817 μm .; width mostly 5 to 10 cells, up to 20 cells wide in *R. pyrifer*. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 17–40 μm . Simply perforated ray cells in *R. angustifolia* (SJRw 34111). Fiber-tracheids and libriform fibers moderately long (1320–1836 μm .; average 1578 μm .) with very thin to thick walls, 3–7 μm .; septate. F/V ratio averages 1.60, range 1.42–1.82. Prismatic crystals occasional to absent in both types of ray cells; no integuments observed; not in chambered cells. Reddish-brown deposits common in rays and fibrous elements.

Zuelania A. Richard. Four or five species from Central America, West Indies, and Venezuela. Five specimens representing one species.

Pore diameter moderately small (64–91 μm .; average 78 μm .); pores average 50 per cent solitary, range 31 to 62 per cent; radial multiples mostly 2, occasionally to 9; pores per square millimeter mostly numerous to very numerous (19–54 pores/mm.²; average 29 pores/mm.²). Vessel elements medium-sized to moderately long (770–1088 μm .; average 964 μm .); perforation plates exclusively simple; end-wall angles 20° to 45°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; small, 4–5 μm . Height of multiseriate portion of rays averages 1276 μm ., range 537–1637 μm .; width mostly 2 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 20–35 μm . Simply perforated ray cells in *Z. guidonia* (MADw 5771, MADw 9882, and SJRW 16644). Fiber-tracheids and libriform fibers medium-sized to moderately long (1168–1790 μm .; average 1569 μm .) with mostly thin to thick walls, 3–7 μm .; septate. F/V ratio averages 1.62, range 1.52–1.73. Prismatic crystals usually abundant in both types of ray cells; integumented; not in chambered cells.

Osmelia Thwaites. Four to 12 species from Ceylon, Malay Peninsula and Archipelago, Philippine Islands, and New Guinea. Six specimens representing two species.

Pore diameter mostly moderately small (56–105 μm .; average 79 μm .); pores average 58 per cent solitary, range 32 to 82 per cent; radial multiples mostly 2, occasionally to 6; pores per square millimeter moderately numerous to mostly numerous (17–42 pores/mm.²; average 28 pores/mm.²). Vessel elements very long to extremely long (1249–2029 μm .; average 1607 μm .); perforation plates mostly simple and rarely scalariform with up to 15 or more bars; end-wall angles 10° to 65°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; very

small to small, 3–5 μm . Height of multiseriate portion of rays averages 1415 μm ., range 971–2293 μm .; width 1 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 17–40 μm . Simply and scalariformly perforated ray cells in *O. grandistipulata* (SJRw 16046 and SJRW 16048) and *O. philippina* (USw 29390). Fiber-tracheids and libriform fibers very long (2317–2991 μm .; average 2583 μm .) with thin to thick walls, 4–8 μm .; septate. F/V ratio averages 1.62, range 1.47–1.86. Prismatic crystals usually abundant or frequent in ray cells of multiseriate portion and occasional or absent in upright ray cells; not integumented; not in chambered cells.

Ophiobotrys Gilg. Monotypic genus from tropical West Africa. One specimen.

Pore diameter moderately small (64–88 μm .; average 74 μm .); pores average 65 per cent solitary; radial multiples mostly 2, occasionally to 3; pores per square millimeter numerous (21 pores/mm.²). Vessel elements moderately long to extremely long (854–2257 μm .; average 1462 μm .); perforation plates exclusively simple; end-wall angle 20° to 35°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; very small, 2–4 μm . Height of multiseriate portion of rays averages 802 μm ., maximum 1160 μm .; width 2 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 17–24 μm . Libriform fibers moderately long to very long (1830–2745 μm .; average 2231 μm .) with mostly very thick walls, 6–9 μm .; septate. F/V ratio averages 1.53. Prismatic crystals abundant in upright ray cells and frequent to occasional in ray cells of multiseriate portion; integumented; not in chambered cells.

Lunania Hooker. Eighteen to 20 species from West Indies, Central America, and tropical South America. Four specimens representing two species.

Pore diameter moderately small (54–97 μm .; average 70 μm .); pores average 55 per cent solitary, range 44 to 77 per cent; radial multiples mostly 2 and 3, occasionally to 6; pores per square millimeter numerous to very numerous (35–42 pores/mm.²; average 38 pores/mm.²). Vessel elements moderately long to very long (1034–1388 μm .; average 1207 μm .); perforation plates exclusively simple; end-wall angles 30° to 45°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; very small to small, 3–6 μm . Height of multiseriate portion of rays averages 1386 μm ., range 758–2124 μm .; width 2 to 4 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to rectangular; cell height 20–35 μm . Fiber-tracheids and libriform fibers moderately long (1715–2111 μm .; average 1889 μm .) with thin to very thick walls, 3–7 μm .; septate. F/V ratio averages 1.57, range 1.50–1.75. Prismatic crystals abundant or frequent in both types of ray cells; integumented; not in chambered cells.

Tetrathylacium Poeppig & Endlicher. Four to five species from Central America and west tropical South America. Two specimens representing two species.

Pore diameter moderately small (64–84 μm .; average 74 μm .); pores average 58 per cent solitary, range 43 to 72 per cent; radial multiples mostly 2, occasionally to 6; pores per square millimeter numerous (24–38 pores/mm.²; average 31 pores/mm.²). Vessel elements very long (1278–1334 μm .; average 1251 μm .); perforation plates exclusively scalariform with up to 15 or more bars which are 2–4 μm . thick and 4–16 μm . apart; end-wall angles 10° to 25°. Occasional tyloses occur in *T. johansenii*. Intervascular pitting alternate; pits circular to polygonal, occasionally oblong; mostly medium-sized, 8–10 μm .; occasionally very large, up to 18 μm . in *T. macrophyllum*. Vessel-ray pits circular to linear; medium to coarse, 8–26 μm . Height of multiseriate portion of rays averages 1432 μm .; range 1077–1787 μm .; width 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 20–35 μm . Fiber-tracheids and libriform fibers moderately long (2010–2158 μm .; average 2084 μm .) with very thin to thin walls, 3–6 μm .; septate. F/V ratio averages 1.67, range 1.56–1.76. In *T. johansenii* prismatic crystals abundant in both types of ray cells; integumented; occasionally in 2-chambered upright ray cells. In *T. macrophyllum*, prismatic crystals abundant in upright ray cells and occasional in ray cells of multiseriate portion; integumented; not in chambered cells.

Samyda Jacquin. Sixteen to 30 species from Mexico and West Indies. Two specimens representing two species.

Pore diameter very small (29–38 μm .; average 34 μm .); pores average 65 per cent solitary, range 56 to 74 per cent; radial multiples mostly 2, occasionally to 6; pores per square millimeter very numerous (72–120 pores/mm.²; average 96 pores/mm.²). Vessel elements medium-sized (548–649 μm .; average 599 μm .); perforation plates exclusively simple; end-wall angles 20° to 45°. Intervascular and vessel-ray pitting alternate; pits circular to polygonal; very small, 2–4 μm . Height of multiseriate portion of rays averages 601 μm .; range 633–669 μm .; width 2 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 20–28 μm . Fiber-tracheids and libriform fibers mostly medium-sized (874–1161 μm .; average 1013 μm .) with thin to thick walls, 3–5 μm .; septate. F/V ratio averages 1.69, range 1.58–1.79. Prismatic crystals frequent in ray cells of multiseriate portion and occasional to rare in upright ray cells; integumented; not in chambered cells.

Neoptychocarpus Buchheim. Two species from tropical South America. Two specimens representing one species.

Pore diameter very small (31–38 μm .; average 34 μm .); pores average 58 per cent solitary; radial multiples mostly 2, occasionally to 7; pores per square millimeter very numerous (73–81 pores/mm.²; average 76

pores/mm.²). Vessel elements moderately long to very long (966–1327 μm .; average 1146 μm .); perforation plates exclusively scalariform with up to 15 or more bars which are 2 μm . thick and 3–5 μm . apart; end-wall angles 10° to 20°. Intervascular and vessel-ray pitting alternate to sometimes opposite; pits circular to oval; very small, 2–4 μm . Height of multiseriate portion of rays averages 1882 μm ., range 1128–2635 μm .; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 28–40 μm . Libriform fibers moderately long (1669–1953 μm .; average 1811 μm .) with thick walls, 10–14 μm .; septate. F/V ratio averages 1.60, range 1.47–1.73. Prismatic crystals abundant in ray cells of multiseriate portion and occasional to absent in upright ray cells; integumented; not in chambered cells. Reddish-brown deposits abundant in ray cells.

Tribe Prockieae (Tiliaceae)

Prockia P. Browne ex Linnaeus. Three to 18 species from the West Indies, tropical America, and Argentina. Two specimens representing one species.

Pore diameter very small to moderately small (42–56 μm .; average 49 μm .); pores 38 per cent solitary, range 23 to 53 per cent; radial multiples and/or radial pore chains mostly 2, 3, and 4, occasionally to 14; pores per square millimeter very numerous (42–92 pores/mm.²; average 67 pores/mm.²). Vessel elements medium-sized (695–740 μm .; average 718 μm .); perforation plates exclusively simple; end-wall angles 15° to 45°. Intervascular and vessel-ray pits alternate; circular to polygonal; small, 4–7 μm . Height of multiseriate portion of rays averages 310 μm ., range 270–350 μm .; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 12–16 μm . Fiber-tracheids and libriform fibers medium-sized (1102–1282 μm .; average 1192 μm .) with mostly thin walls, 3–5 μm .; septate. F/V ratio averages 1.66, range 1.59–1.73. Prismatic crystals abundant to frequent in upright ray cells and occasional to absent in ray cells of multiseriate portion; integumented; mostly in 2-chambered to rarely 4-chambered upright ray cells. Reddish-orange deposits abundant in rays of *P. crucis* (MADw 21831).

Hasseltia H.B.K. Ten to 12 species from Mexico, Central America, and tropical South America. Six specimens representing four species.

Pore diameter moderately small (51–95 μm .; average 63 μm .); pores average 60 per cent solitary, range 38 to 71 per cent; radial multiples mostly 2, occasionally to 5; pores per square millimeter numerous to very numerous (32–110 pores/mm.²; average 54 pores/mm.²). Vessel elements moderately long to very long (832–1250 μm .; average 1073 μm .); perforation plates in *H. floribunda* mostly simple and occasionally scalariform with vestigial and up to 6 bars; exclusively simple in all other specimens of *Hasseltia*; end-wall angles 20° to 35°. Tyloses occur occasionally in

H. floribunda (MADw 12427), *H. lateriflora* (SJRw 20891), and *H. laxiflora*. Fine spiral thickenings rarely occur in the vessel tails of *H. floribunda* (SJRw 12427), *H. lateriflora*, and *H. cf. guatemalensis*. Intervascular pitting alternate; pits circular to polygonal; small, 4–7 μm . Vessel-ray pits circular to linear; fine to coarse, 4–30 μm . Height of multiseriate portion of rays averages 544 μm ., range 298–765 μm .; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 15–27 μm . Simply perforated ray cells in *H. floribunda* (SJRw 12427), *H. lateriflora*, and *H. laxiflora*. Fiber-tracheids and libriform fibers medium-sized to moderately long (1416–2014 μm .; average 1821 μm .) with very thin to thin walls, 3–6 μm .; septate. F/V ratio averages 1.70, range 1.43–1.91. Prismatic crystals usually abundant to frequent in upright ray cells and occasional to rare in ray cells of multiseriate portion; in *H. laxiflora* crystals are abundant in both types of ray cells; in *H. cf. guatemalensis* crystals are rare in upright ray cells and absent in ray cells of multiseriate portion; all specimens of *Hasseltia* have prismatic crystals that are integumented and mostly in 2- to occasionally 4-chambered upright ray cells. Druse crystals rarely to occasionally in procumbent and 4-chambered upright ray cells of *H. floribunda* (MADw 5747). Reddish-yellow deposits frequent in ray cells of *H. laxiflora*.

Pleuranthodendron L. O. Williams. One to four species from Mexico, Central America, and tropical South America. Six specimens representing one species.

Pore diameter moderately small (52–84 μm .; average 70 μm .); pores average 49 per cent solitary, range 30 to 74 per cent; radial multiples mostly 2 and 3, occasionally to 8; pores per square millimeter numerous to very numerous (32–68 pores/mm.²; average 44 pores/mm.²). Vessel elements medium-sized to moderately long (739–1067 μm .; average 971 μm .); perforation plates simple and scalariform with up to 7 bars which are 2–4 μm . thick and 4–20 μm . apart; end-wall angles 20° to 50°. Fine spiral thickenings occur in the vessel tails. Intervascular pitting alternate; pits circular, occasionally linear; mostly medium-sized, 8–10 μm ., occasionally very large, up to 40 μm . Vessel-ray pits circular to linear; medium to coarse, 8–32 μm . Height of multiseriate portion of rays averages 585 μm ., range 301–838 μm .; width 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 13–23 μm .; in *P. mexicana* (MADw 11004) cell height 18–28 μm . Scalariformly perforated ray cells common. Fiber-tracheids and libriform fibers medium-sized to moderately long (1436–1907 μm .; average 1684 μm .) with thin to thick walls, 3–6 μm .; septate. F/V ratio averages 1.74, range 1.57–1.94. Prismatic crystals more abundant in upright ray cells than in ray cells of multiseriate portion; integumented; mostly in 2-chambered upright ray cells, not in chambered cells in *P. mexicana* (MADw 11004). Reddish-brown deposits common in ray cells.

Macrohasseltia L. O. Williams. Monotypic genus from Central America. Two specimens.

Pore diameter moderately small (86–90 μm .; average 88 μm .); pores average 48 per cent solitary, range 36 to 60 per cent; radial multiples mostly 2 and 3, occasionally to 6; pores per square millimeter moderately numerous (17–20 pores/ mm^2 ; average 18 pores/ mm^2). Vessel elements moderately long (816–1121 μm .; average 968 μm .); perforation plates mostly simple and occasionally scalariform with vestigial and up to 6 bars; end-wall angles 25° to 50° . Tyloses frequent in *M. macroterantha* (MADw 10286). Fine spiral thickenings occur in the vessel tails and occasionally throughout the vessel elements. Intervascular pitting alternate; pits circular to occasionally linear; mostly large, 10–14 μm ., occasionally very large, up to 40 μm . Vessel-ray pits circular to linear; coarse, 10–22 μm . Height of multiseriate portion of rays averages 223 μm . or 10 cells, range 220–226 μm .; width 2 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 17–28 μm . Simply perforated ray cells in *M. macroterantha* (MADw 10286). Fiber-tracheids and libriform fibers medium-sized to moderately long (1491–1877 μm .; average 1684 μm .) with thin walls, 3–5 μm .; septate. F/V ratio averages 1.75, range 1.67–1.83. Prismatic crystals abundant to occasional in upright ray cells and absent in ray cells of multiseriate portion; integumented; mostly in 2-chambered upright ray cells. Reddish-brown deposits abundant in ray cells of *M. macroterantha* (MADw 10305).

Anomalous Genera

The genera described in this category were once placed in the Flacourtiaceae, but now are not considered by most taxonomists as belonging to this family. The following descriptions are complete descriptions and no characters are deleted.

Ancistrothyrsus Harms (Passifloraceae). Monotypic genus from western tropical America. One specimen.

Growth rings poorly defined to somewhat distinct. Pores mostly circular in outline; tangential diameter medium-sized to moderately large (174–260 μm .; average 228 μm .); pores average 89 per cent solitary; radial multiples mostly 2; pores per square millimeter moderately few (6 pores/ mm^2). Vessel elements medium-sized to moderately long (366–1037 μm .; average 728 μm .); perforation plates mostly simple and occasionally scalariform with a few vestigial bars; end-wall angles 30° to 90° . Vessel-wall thickness 6 μm . Tyloses present, occasionally sclerotic; sometimes prismatic crystals in tyloses. Intervascular pitting alternate; pits mostly circular; medium-sized, 8–10 μm . Vessel-ray pits circular to somewhat oblong; medium to coarse, 8–14 μm . Rays of two types, uniseriate homocellular rays composed entirely of upright ray cells and multiseriate heterocellular rays with long uniseriate extensions (Heterogeneous

Types I and IIA, Kribs 1935). Height of multiseriate portion of rays averages 2157 $\mu\text{m.}$, maximum 5185 $\mu\text{m.}$; width 3 to 7 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 30–40 $\mu\text{m.}$ Imperforate tracheary elements are tracheids; medium-sized to moderately long (1037–1738 $\mu\text{m.}$; average 1418 $\mu\text{m.}$) with thin to thick walls, 5–7 $\mu\text{m.}$; nonseptate. F/V ratio 1.95. Axial parenchyma abundant; vasicentric to somewhat aliform and apotracheal diffuse. Prismatic crystals occasional in axial parenchyma; frequent in ray cells of multiseriate portion and rare in upright ray cells; not integumented; not in chambered cells. Brown to reddish-brown deposits frequent to occasional in axial and ray parenchyma.

Barteria Hooker f. (Passifloraceae). Five to seven species from tropical Africa. One specimen.

Growth rings poorly defined. Pores circular to oval in outline; tangential diameter medium-sized (144–192 $\mu\text{m.}$; average 164 $\mu\text{m.}$); pores average 34 per cent solitary; radial multiples mostly 2, 3, and 4, occasionally to 6; pores per square millimeter moderately few (6 pores/ mm.^2). Vessel elements moderately long to very long (793–1708 $\mu\text{m.}$; average 1190 $\mu\text{m.}$); perforation plates mostly simple and occasionally scalariform with vestigial and up to 12 bars which are 2–4 $\mu\text{m.}$ thick and 4–10 $\mu\text{m.}$ apart; end-wall angles 35° to 50°. Vessel-wall thickness 2–6 $\mu\text{m.}$ Intervascular and vessel-ray pitting alternate; pits circular to oval; small to medium-sized, 5–8 $\mu\text{m.}$ Rays of two types, uniseriate homocellular rays composed entirely of upright ray cells and multiseriate heterocellular rays with long uniseriate extensions (Heterogeneous Type I, Kribs 1935). Height of multiseriate portion of rays averages 624 $\mu\text{m.}$, maximum 840 $\mu\text{m.}$; width 1 to 3 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to elongate; cell height 35–55 $\mu\text{m.}$ Imperforate tracheary elements are libriform fibers; moderately long to extremely long (1860–3263 $\mu\text{m.}$; average 2511 $\mu\text{m.}$) with very thick walls, 9–12 $\mu\text{m.}$; nonseptate. F/V ratio 2.11. Axial parenchyma abundant; vasicentric and apotracheal in short tangential lines (reticulate). Prismatic crystals absent. Reddish to yellowish-brown deposits abundant in rays.

Paropsia Noronha ex Thouars (Passifloraceae). Thirteen to 20 species from tropical Africa, Madagascar, Sumatra, and the Malay Peninsula. Four specimens representing four species.

Growth rings poorly defined to absent. Pores circular to oval in outline; tangential diameter moderately small to medium-sized (79–138 $\mu\text{m.}$; average 111 $\mu\text{m.}$); pores average 52 per cent solitary, range 37 to 70 per cent; radial multiples mostly 2 and 3, occasionally to 10; pores per square millimeter few to moderately numerous (4–18 pores/ mm.^2 ; average 12 pores/ mm.^2). Vessel elements medium-sized to very long (655–1735 $\mu\text{m.}$; average 966 $\mu\text{m.}$); perforation plates exclusively simple; end-wall angles 30° to 50°. Vessel-wall thickness 4–6 $\mu\text{m.}$ Intervascular and vessel-ray

pitting alternate; pits circular to oval; very small to small, 3–5 μm ., in *P. braunii* and *P. guineensis* and small to medium-sized, 6–8 μm ., in *P. madagascariensis* and *P. vareciformis*. Rays variable; mostly multiseriate homocellular rays or occasionally heterocellular rays with short uniseriate extensions (Heterogeneous Types I and IIA or Homogeneous Type I, Kribs 1935). Height of multiseriate portion of rays averages 2077 μm ., range 979–3327 μm .; width 2 to 5 cells. Individual ray cells of multiseriate portion as observed on the radial surface are square to occasionally elongate; cell height 23–55 μm . Simply perforated ray cells in *P. braunii*. Imperforate tracheary elements fiber-tracheids and libriform fibers; mostly very long to extremely long (2115–3884 μm .; average 2570 μm .) with very thick walls, 5–14 μm .; nonseptate. F/V ratio averages 2.82, range 2.24–3.23. Axial parenchyma abundant, apotracheal in short tangential lines (reticulate). Large prismatic crystals (\approx 40 μm .) occur occasionally in axial parenchyma of *P. braunii* and *P. vareciformis*. Prismatic crystals generally more frequent in ray cells of multiseriate portion than in upright ray cells; no integuments observed; not in chambered cells. Reddish-brown deposits abundant in the axial and ray parenchyma of *P. guineensis* and *P. vareciformis*.

Soyauxia Oliver (Medusandraceae or Passifloraceae). One to seven species from tropical West Africa. One specimen.

Growth rings poorly defined. Pores angular in outline; tangential diameter moderately small (64–80 μm .; average 72 μm .); pores average 100 per cent solitary; pores per square millimeter numerous (21 pores/ mm^2). Vessel elements very long to mostly extremely long (1769–2653 μm .; average 2168 μm .); perforation plates exclusively scalariform, mostly over 15 bars which are 2–3 μm . thick and 6–10 μm . apart; end-wall angles 10° to 25° . Vessel-wall thickness 3–4 μm . Intervascular pits absent except on overlapping vessel-element ligules; no definite arrangement observed; medium-sized, 6–10 μm . Vessel-ray pits circular to linear; medium to mostly coarse; 8–36 μm . Rays uniseriate and heterocellular (Heterogeneous Type III, Kribs 1935); height averages 471 μm . or 17 cells, maximum 720 μm . or 27 cells. Individual ray cells as observed on the radial surface are square toward the middle of the rays and upright toward the end of the rays; square cell height 25–35 μm . Imperforate tracheary elements are tracheids; very long to extremely long (2318–2660 μm .; average 2912 μm .) with mostly very thick walls, 7–10 μm .; nonseptate. F/V ratio 1.34. Axial parenchyma apotracheal in short tangential lines (reticulate) and diffuse. Prismatic crystals absent. Silica bodies abundant in square ray cells and occasionally in upright ray cells; 10–14 μm . in diameter. Reddish-brown deposits abundant in rays and fibrous elements.

Peridiscus Benth (Peridiscaceae). Monotypic genus from Venezuela and Brazil. One specimen.

Growth rings absent. Pores circular to somewhat angular in outline;

tangential diameter mostly medium-sized (96–120 μm .; average 109 μm .); pores 45 per cent solitary; radial multiples mostly 2 and 3, occasionally to 5; pores per square millimeter moderately numerous (14 pores/ mm^2). Vessel elements very long to extremely long (1550–2978 μm .; average 2218 μm .); perforation plates exclusively scalariform, up to 15 or more bars which are 4–6 μm . thick and 8–12 μm . apart; end-wall angles 15° to 30°. Vessel-wall thickness 4–6 μm . Tyloses abundant to frequent. Intervascular pitting opposite; pits circular to oval; large to mostly very large, 14–18 μm . Vessel-ray pits circular to linear; coarse, 10–20 μm . Rays of two types: uniseriate homocellular rays composed entirely of upright cells and multiseriate heterocellular rays with long uniseriate extensions (Heterogeneous Type I, Kribs 1935). Height of multiseriate portion of rays averages 1707 μm ., maximum 2947 μm .; width 1 to 2 cells. Individual ray cells of multiseriate portion as observed on the radial surface are mostly square; cell height 33–53 μm . Imperforate tracheary elements libriform fibers; very long to extremely long (2448–3794 μm .; average 3134 μm .) with very thick walls, 9–15 μm .; septate in part. F/V ratio 1.41. Axial parenchyma abundant; apotracheal in short tangential lines (reticulate) and diffuse. Prismatic crystals absent. White deposits occasionally occur in vessels and reddish-brown deposits are frequent in rays.

Aphloia (DC.) Bennett (= *Neumannia*, Neumanniaceae). Four to six species from tropical East Africa, Madagascar, Seychelles Islands, and Mascarene Islands. Four specimens representing two species.

Growth rings poorly defined. Pores circular to angular in outline; tangential diameter moderately small to medium-sized (78–120 μm .; average 94 μm .); pores average 97 per cent solitary; radial multiples occasionally to 2; pores per square millimeter numerous to very numerous (32–61 pores/ mm^2 ; average 43 pores/ mm^2). Vessel elements mostly very long to extremely long (1051–2416 μm .; average 1452 μm .); perforation plates exclusively scalariform; in *A. theiformis* (SJRw 32941) mostly scalariform and occasionally simple, mostly over 15 bars which are 2–4 μm . thick and 2–8 μm . apart; end-wall angles 15° to 25°. Vessel-wall thickness 2–4 μm . Fine spiral thickenings present in vessel-element tails; occasionally to rarely throughout the vessel elements. Intervascular pitting alternate; pits circular to oval; small, 6–7 μm . Vessel-ray pits circular to occasionally linear; medium to coarse, 4–20 μm . Rays of two types: uniseriate homocellular rays composed entirely of upright cells and heterocellular multiseriate rays with long uniseriate extensions (Heterogeneous Type I, Kribs 1935). Height of multiseriate portion of rays averages 3666 μm ., range 2711–4795 μm .; width 4 to 30 cells or 96–520 μm . (mostly 191–349 μm .). Individual ray cells of multiseriate portion as observed on the radial surface are mostly elongate; cell height 19–32 μm . Scalariformly perforated ray cells occur in *A. theiformis* (SJRw 32941). Imperforate tracheary elements fiber-tracheids; medium-sized to moderately long (1329–2214 μm .; average 1860 μm .) with mostly

thin to thick walls, 5–8 μm .; in *A. theiformis* (SJRw 32914), thick to very thick, 11–13 μm .; septate. F/V ratio averages 1.80, range 1.72–1.85. Axial parenchyma rare to frequent; vasicentric and apotracheal diffuse. Prismatic crystals absent. Reddish-brown deposits abundant in rays.

Asteropeia Thouars (Theaceae or Asteropeiaceae). Six to seven species from Madagascar. Three specimens representing two species.

Growth rings absent. Pores circular to oval in outline; tangential diameter moderately small to mostly medium-sized (91–190 μm .; average 156 μm .); pores average 97 per cent solitary; range 93 to 100 per cent; radial multiples occasionally to 2; pores per square millimeter in *A. rhopaloides* moderately few (5–7 pores/mm.²); in *A. micraster* numerous (24 pores/mm.²). Vessel elements medium-sized (556–670 μm .; average 627 μm .); perforation plates exclusively simple; end-wall angles 60° to 70°. Vessel-wall thickness 4–6 μm . Intervascular pits essentially absent except on the vessel-element ligules; alternate; very small, 2–4 μm . Vessel-ray pits circular to oval; fine, 2–4 μm . Rays mostly uniseriate, rarely biseriate, and homocellular (Homogeneous Type III, Kribs 1935); height averages 194 μm . or 7 cells, range 122–241 μm . or 6 to 9 cells. Individual procumbent cells as observed on the radial surface are elongate; cell height 12–25 μm . Imperforate tracheary elements fiber-tracheids; very short to medium-sized (828–1146 μm .; average 1015 μm .) with very thick walls, 4–10 μm .; nonseptate. F/V ratio averages 1.61, range 1.49–1.71. Axial parenchyma abundant; aliform to confluent. Prismatic crystals absent. Yellowish deposits abundant to occasional in vessels; in *A. micraster* and *A. rhopaloides* (SJRw 33869) deposits occur in axial and ray parenchyma.

Lethedon Sprengel (= *Microsemma* Labillardière Thymelaeaceae). Eleven species from New Caledonia and Queensland, Australia. Two specimens representing two species.

Growth rings poorly defined. Pores circular to oval in outline; tangential diameter moderately small to medium-sized (72–121 μm .; average 96 μm .); pores average 56 per cent solitary, range 33 to 79 per cent; radial multiples mostly 2, occasionally to 8; pores per square millimeter moderately numerous to numerous (13–22 pores/mm.²; average 18 pores/mm.²). Vessel elements medium-sized (447–625 μm .; average 536 μm .); perforation plates exclusively simple; end-wall angles 25° to 70°. Vessel-wall thickness 4–6 μm . Intervascular and vessel-ray pitting alternate; pits circular to oval; small, 4–7 μm . Rays uni- or biseriate and homocellular or heterocellular with 1 to 3 rows of upright cells (Heterogeneous Type IIA and Homogeneous Type I, Kribs 1935). Excluding upright ray cells, ray height averages 928 μm ., range 734–1122 μm .; individual ray cells as observed on the radial surface are square to elongate; cell height 26–40 μm . Imperforate tracheary elements tracheids; medium-sized (1175–1420 μm .; average 1298 μm .) with thin to thick walls, 5–8 μm .; nonseptate. F/V ratio averages 2.44, range 2.27–2.62. Axial paren-

chyma frequent; aliform to confluent. Prismatic crystals rare in upright ray cells and occasional to frequent in other ray cells; no integuments observed; not in chambered cells. Crystals absent in *L. setosa*.

Triphyophyllum Airy Shaw (= *Dioncophyllum*, Dioncophyllaceae). Monotypic genus from Sierra Leone, Liberia, and Ivory Coast. Description based on work by Metcalfe (1952) and one specimen.

Growth rings absent. Pores mostly circular in outline; tangential diameter medium-sized to very large (165–350 μm .; average 300 μm .); pores mostly solitary; radial multiples occasionally to 2; pores per square millimeter very few to few (about 2 pores/ mm^2). Vessel elements moderately short to medium-sized (286–530 μm .; average 412 μm .); perforation plates exclusively simple; end-wall angles slightly oblique to transverse. Vessel-wall thickness 12–16 μm . Intervascular pits rare and similar to vessel-ray pits; mostly alternate; circular to oval; medium-sized to large, 8–12 μm .; often with coalescent apertures. Rays uniseriate and homocellular, entirely composed of square or upright cells (Homogeneous Type III, Kribs 1935); height short to moderately high. Imperforate tracheary elements fiber-tracheids; very short to medium-sized (653–1102 μm .; average 861 μm .) with thin to thick walls; nonseptate. F/V ratio 2.09. Axial parenchyma frequent; vasicentric and apotracheal diffuse. Prismatic crystals absent.

DISCUSSION

COMPARATIVE ANATOMY OF THE SECONDARY XYLEM WITHIN FLACOURTIACEAE

The xylem anatomy of Flacourtiaceae supports Dr. Hermann Sleumer's contention (personal communication) that the "Flacourtiaceae as a family is a fiction; only the tribes are homogeneous." Morphologically and anatomically, only a combination of characters can be used to circumscribe and define Flacourtiaceae. Features of the wood common to most genera include the absence of axial parenchyma, presence of septate fibrous elements, heterocellular rays with long uniseriate extensions, moderately small to medium-sized pore diameters, medium-sized to very long vessel and fibrous elements, a fibrous-element length to vessel-element length ratio of less than two, and prismatic crystals in the ray cells. Two of the more conspicuous features which vary are the vessel pits and perforation plates. By combining these two variable features, I have been able to define six anatomical categories or groups into which the genera of Flacourtiaceae can be placed. Genera in groups I, II, and III have medium-sized to very large (7– over 15 μm .) intervacular pits and medium to coarse (7– over 10 μm .) vessel-ray pits. In addition, the intervacular and vessel-ray pits do not have similar shapes. These combinations of pitting are called *large vessel pitting* throughout the remainder of the text (FIGURES 24, 25). Genera in group I have exclusively scalariform perforation plates; genera in group II have simple and scalariform perforation

plates; and genera in group III have exclusively simple perforation plates. Groups IV, V, and VI have intervacular pits that are similar in size and shape to the vessel-ray pits. Since the intervacular and vessel-ray pits are generally very small or small ($< 8 \mu\text{m.}$), this pitting is called *small vessel pitting* throughout the remainder of the text (FIGURES 26, 27). Genera of Group IV have exclusively scalariform perforation plates; genera of group V have simple and scalariform perforation plates; and genera of group VI have exclusively simple perforation plates. In APPENDIX I each genus of the Flacourtiaceae is assigned to one or two of the six groups just described.

For the most part, the two different pit sizes are specific for the tribes of Flacourtiaceae. The tribes Berberidopsideae, Pangieae, and Oncobeeae contain genera with large vessel pits (groups I, II, and III); whereas the tribes Scolopieae, Homalieae, Banareae, and Casarieae (except *Tetra-thylacium*) have genera with small vessel pits (groups IV, V, VI).

The tribe Flacourtieae has seven genera with large vessel pits and four with small vessel pits. Although there are other features in the secondary xylem which further separate these genera, no single taxonomic character or combination of characters suggests that the genera of tribe Flacourtieae with large vessel pitting should be separated from those genera with small vessel pitting. Thus, anatomically the Flacourtieae appears to be a transitional group linking the tribes with large vessel pits to the tribes with small vessel pits. Since there appears to be a continuum, the Flacourtiaceae must be considered as a large heterogeneous family. However, future investigations in chemotaxonomy, morphology, palynology, and other fields may help to define more precisely the subfamilial or familial rankings of the tribes comprising the Flacourtiaceae.

EVOLUTIONARY TRENDS WITHIN FLACOURTIACEAE

For the most part, the secondary xylem supports the phylogenetic sequences of tribes of Flacourtiaceae that were proposed by Warburg (1894) and Gilg (1925). Since the six anatomical groups generally conform to the tribes of Flacourtiaceae, I attempted to determine the phylogeny of the anatomical groups independently of the sequences of Warburg and Gilg. The only assumption which guided my comparisons is that the family Flacourtiaceae is monophyletic in origin.

Bailey and Tupper (1918) established conclusively that within a given taxon simple perforation plates were more specialized than scalariform perforation plates. Consequently, genera of group I which have many bars, or genera of group IV which have small vessel pits and exclusively scalariform perforation plates with many bars appear to be the most primitive. When the floral characteristics and other features of the secondary xylem (APPENDIX I) are examined in the genera of group I (mostly in the Berberidopsideae), characters such as spirally arranged flower parts, numerous sepals and stamens, occasionally opposite intervacular pitting, and generally very long vessel elements are found to be present.

In contrast, *Neoptychocarpus* (tribe Caseariae), the only genus of group IV, has more specialized structures, such as whorled flower parts, four sepals and no petals, eight stamens, and moderately long vessel elements. Therefore, group I is potentially the most primitive of the six anatomical groups.

Frost (1930b) demonstrated evolutionary trends from exclusively scalariform perforation plates with many bars to exclusively scalariform perforation plates with fewer bars, to simple and scalariform perforation plates, to exclusively simple perforation plates. Thus group I, which has exclusively scalariform perforation plates, may have given rise to group II, which has simple and scalariform perforation plates. Also, group III, which has exclusively simple perforation plates, is more specialized than either groups I or II. Groups with small vessel pits also could have evolved in a like manner, but *Neoptychocarpus*, the only genus of group IV, is morphologically rather specialized for the Flacourtiaceae. In addition, the wood anatomy of *Neoptychocarpus* appears to show affinities with the family Lacistemaceae, which is discussed later. It seems that unless *Neoptychocarpus* is derived from some nonflacourtiaceous group, it probably evolved from the genera in group I, since the genera of both these groups have exclusively scalariform perforation plates. Whether the genera of groups V and VI evolved from *Neoptychocarpus* or directly from group I or II cannot be determined with certainty. However, assuming a monophyletic origin for Flacourtiaceae, genera with large vessel pits appear to have given rise to genera with small vessel pits.

If we compare the generic composition of the six anatomical groups to the flacourtiaceous tribes of Gilg (1925), Warburg (1894), and Hutchinson (1967), many similarities are noted. In FIGURE 1 the phylogenetic sequence of Gilg's tribes is shown along with the number of genera represented by each anatomical group. Basing his conclusions primarily on gross morphology, Gilg considered the tribe Oncobeeae to be the most primitive. Anatomically, Gilg's Oncobeeae has several genera with exclusively scalariform perforation plates and large vessel pits (group I). Thus the wood anatomy substantiates the primitive position of Oncobeeae. Warburg (1894) and Hutchinson (1967) considered the genera of Gilg's Oncobeeae to constitute the base for two separate tribes. Warburg called his tribes Erythrospemeae and Oncobeeae and considered the Erythrospemeae to be the most primitive (FIGURE 1). Hutchinson's two tribes are the Oncobeeae and Berberidopsidaeae, the latter of which he considered the most primitive. The genera of Berberidopsidaeae or Erythrospemeae belong mainly to group I, while the genera of Oncobeeae belong mainly to group II (APPENDIX I). Consequently, the wood anatomy not only supports the splitting of Gilg's tribe Oncobeeae into two separate tribes, but it also supports the phylogenetic specialization from group I (Warburg's Erythrospemeae) to group II (Warburg's Oncobeeae) (FIGURE 1).

As shown in FIGURE 1, the tribe Pangieae is more specialized than either of its possible ancestors, the Erythrospemeae or Oncobeeae. Both these primitive tribes are characterized by genera in group I, but tribe

Pangieae is characterized by genera mostly in groups II and III. As proposed, genera of group I probably gave rise to genera in groups II and III. Thus, the wood structure confirms this part of the sequences.

The tribe Scolopieae is derived from the tribe Oncobaeae. The genera of Gilg's Scolopieae belong to groups I, II, III, V, and VI; however, Hutchinson (1967) placed most of these genera elsewhere. Genera in Hutchinson's Scolopieae and Banareae (formed from genera in Gilg's Scolopieae) are in groups V and VI. As proposed, group VI is the most specialized group, since genera with small vessel pits are derived from genera with large vessel pits and group VI has exclusively simple perforation plates. Thus, the xylem anatomy cannot negate the evolution of the Scolopieae (genera with small vessel pits) from the Oncobaeae (genera with large vessel pits).

The tribe Homalieae is derived from the Scolopieae. Since the genera of Homalieae belong mostly to group VI, the secondary xylem cannot negate the derivation of tribe Homalieae from the Scolopieae. As discussed later, the wood of Homalieae, Banareae, and Scolopieae suggest a close alliance.

As previously mentioned, the Flacourtieae is the only tribe in which some genera have large vessel pits and some have small vessel pits. The phylogenies of Warburg (1894) and Gilg (1925) show tribe Scolopieae as the origin of the Flacourtieae. If Hutchinson's Scolopieae and Banareae replace the Scolopieae of Warburg and Gilg, then the derivation of tribe Flacourtieae from the Scolopieae suggests an interruption in the continuum from large to small vessel pits. Tribe Oncobaeae is characterized by large vessel pits; Hutchinson's Scolopieae and Banareae are characterized by small vessel pits; and tribe Flacourtieae is characterized by both large and small vessel pits. Thus, the secondary xylem indicates need for a change from the phylogenies of Warburg and Gilg. The anatomy suggests the derivation of both the Flacourtieae and Scolopieae from tribe Oncobaeae. The Flacourtieae would then occupy a transitional position between the tribes characterized by large vessel pits and the tribe Caseariae, which generally has small vessel pits and exclusively simple perforation plates. The xylem anatomy does not negate this derivation of the Caseariae from tribe Flacourtieae.

TRIBAL AND GENERIC ANATOMY

The generic composition of Hutchinson's (1967) Flacourtiaceae generally agrees with evidence from the secondary xylem. Hutchinson's transfer of *Paropsia* and other genera to the Passifloraceae and the reorganization of the genera in Gilg's Scolopieae to form tribes Scolopieae, Banareae, and Prockieae (Tiliaceae) are supported or at least are not negated by the xylem anatomy. The relationships of the tribes of Flacourtiaceae together with their respective genera and a group of "Anomalous Genera" are discussed in detail below.

Tribe Berberidopsidae. The tribe Berberidopsidae is anatomically and

taxonomically the most primitive tribe of the Flacourtiaceae. The woods of genera in this tribe are homogeneous with the exception of *Ahernia*, *Berberidopsis*, and *Streptothamnus*. Of the eight genera examined, only *Ahernia* has the combination of exclusively simple perforation plates and large vessel pits (group III). *Ahernia* also has many other distinctive features (APPENDIX I). These characteristics indicate affinities to certain genera in Flacourtiaceae; however, morphological characters do not conform these supposed affinities to *Ahernia*.

Berberidopsis and *Streptothamnus* are the two most primitive genera in the Flacourtiaceae. Anatomically both genera have nonseptate tracheids (FIGURE 7), approximately 100 per cent solitary pores, and very high rays (over 1.5 cm.). These three characters, coupled with evidence from the floral morphology (Hutchinson 1967), not only ally these two genera, but also seem to put them somewhere between the Flacourtiaceae and Dilleniaceae. Perhaps a new family could be established to contain them. This Dilleniaceae-Flacourtiaceae relationship will be discussed further under FAMILY RELATIONSHIPS.

Tribe Oncobeeae. The genera in the tribe Oncobeeae as formulated by Warburg (1894) or Hutchinson (1967) are scarcely distinguishable anatomically (APPENDIX I) and are related to the genera of the Erythrospemeae (Warburg) or Berberidopsidae (Hutchinson). Evidence which supports the close relationship of tribes Erythrospemeae (Berberidopsidae) and Oncobeeae is the occasional retention of opposite intervascular pitting and exclusively scalariform perforation plates in some species of *Mayna* and *Carpotroche* (Oncobeeae).

After the generic description of *Buchnerodendron*, Hutchinson (1967) stated that it is "an interesting genus providing a definite link with Tiliaceae and resembling a *Sparrmania* [sic]." The wood of *Buchnerodendron* is similar to that in other genera of Oncobeeae. An examination of a specimen of *Sparmannia africana* L. f. (SJRw 33838) from South Africa revealed many differences which militate against any close alliance between *Buchnerodendron* and *Sparmannia*.

Tribe Pangieae. Although the wood anatomy of the genera of Pangieae (excluding *Goethalsia*) is somewhat homogeneous, *Hydnocarpus* (*sensu lato*) seems to be distinct. Hutchinson (1967) considers *Hydnocarpus* and *Taraktogenos* to be separate but related genera; however Warburg (1894), Gilg (1925), and Sleumer (1938, 1954) consider these two genera, together with *Asteriastigma*, as one genus — *Hydnocarpus*. In addition, Schaeffer's (1972) study of pollen morphology supports Sleumer and others. All species of *Hydnocarpus* (*sensu lato*) have exclusively scalariform perforation plates and all species, except *H. sumatrana* (Miq.) Koord., contain vitreous silica (FIGURE 6). Since no anatomical feature could be found to support the segregation of *Hydnocarpus* (*sensu lato*), the xylem anatomy favors the submersion of *Taraktogenos* and *Asteriastigma* in *Hydnocarpus*.

Hydnocarpus is distinctive and primitive in that it is the only genus of

the Pangieae with exclusively scalariform perforation plates and opposite or opposite to alternate intervacular pitting. In addition, *Hydnocarpus* has the lowest fiber length to vessel length ratio (1.56) of the Pangieae, some of the longest vessel and fibrous elements of the Flacourtiaceae, and is the only genus of the Flacourtiaceae producing vitreous silica. Thus, *Hydnocarpus* is undoubtedly the most primitive genus in tribe Pangieae. Based on the structure of the wood, a more likely placement of *Hydnocarpus* would be in either the tribe Berberidopsideae or the Oncobaeae. The floral morphology, however, does not suggest any such transfer, although the pollen morphology does support the view that *Hydnocarpus* is somewhat isolated. Schaeffer (1972) concluded that only *Chlorocarpha* (no wood available) and *Neoptychocarpus* have pollen that is similar to that of *Hydnocarpus*. Although *Neoptychocarpus* is in a different and more advanced tribe (the Casearieae), the wood of *Neoptychocarpus* is not only primitive but is also similar to the wood of *Lacistema*. *Hydnocarpus*, *Neoptychocarpus*, and *Lacistema* do not appear to be closely related florally, but there do seem to be some common bonds which need further examination.

Evidence from chemotaxonomy suggests a link between tribe Oncobaeae and *Hydnocarpus*. Of the genera of tribe Pangieae, only species of *Hydnocarpus* produce chaulmoogra oil (i.e. cyclopentene fatty acids). *Pangium* and *Gynocardia* were once thought to contain chaulmoogra oil, but they are now known to contain the cyanogenetic heteroside, gynocardoside (Alston & Turner 1963). Other genera in the plant world known to contain chaulmoogra oil are *Carpotroche*, *Mayna*, *Lindackeria*, *Oncoba*, and *Caloncoba*, all of which belong to the tribe Oncobaeae. Supposedly Roig and Rodríguez (1944) isolated chaulmoogra oil from some genera in the tribe Casearieae, but Gibbs (1945) stated that only genera in the tribes Pangieae and Oncobaeae contain chaulmoogra oil. With corroborative evidence from chemotaxonomy, pollen morphology, and wood anatomy, it appears that the genus *Hydnocarpus* is somewhat isolated. Also, *Hydnocarpus* has retained some primitive genetic structure of the ancient gene pool from which the tribes Pangieae and Oncobaeae and possibly the genera *Neoptychocarpus* and *Lacistema* may have evolved.

Tribe Scolopieae. As formulated by Hutchinson (1967), the tribe Scolopieae consists of *Scolopia*, *Pseudoscolopia*, and *Dioncophyllum* of Gilg's Scolopieae, the genera of Gilg's tribe Phyllobotryeae, and a few genera described since 1925. Of these nine genera only *Scolopia*, *Bartholomaea*, and *Dioncophyllum* (including *Triphyophyllum*) were available for study. Since *Triphyophyllum* is considered by most taxonomists as an aberrant genus in the Flacourtiaceae, it is discussed later under the heading "Anomalous Genera." Of the other two genera, only *Scolopia* is represented in my study by an ample number of wood specimens. From anatomical features summarized in APPENDIX I, the secondary xylem of *Scolopia* and *Bartholomaea* can be compared. Although a few features are inconsistent, there is enough similarity to conclude that *Scolopia* and *Bartholomaea* are allied and belong in the same tribe.

Tribes Banareae and Homalieae. *Banara* and *Pineda* of Gilg's tribe Scolopieae, together with *Trimeria* of Gilg's tribe Homalieae and the anomalous genus *Asteropeia*, form Hutchinson's new tribe Banareae. Since *Asteropeia* is anomalous, it is considered under "Anomalous Genera." In their xylem anatomy, *Banara*, *Pineda*, and *Trimeria* are so similar that they are scarcely separable on this basis.

Of the seven genera of Homalieae only *Homalium* and *Calantica* were available for study. These two genera have very similar secondary xylem, and in some cases species of *Calantica* cannot be distinguished from some species of *Homalium*.

From the summary of anatomical features in APPENDIX I, a comparison can be made of the xylem anatomy in genera of the Scolopieae, Banareae, and Homalieae. It is apparent that the genera in these three tribes are allied and practically indistinguishable on anatomical grounds. Thus, whether the genera of tribes Banareae and Scolopieae constitute one tribe and two subtribes or two separate tribes or whether the genus *Trimeria* is in the Homalieae or Banareae is strictly a matter for taxonomic judgment.

Tribe Prockieae (Tiliaceae). The placement and relationships of the genera of the Prockieae are not fully understood. Within the Prockieae, *Prockia*, *Hasseltia*, *Pleuranthodendron* (= *Hasseltiopsis*), and *Macrohasseltia* (included here by Williams 1961) were examined (APPENDIX I). *Prockia* belongs in the anatomical group VI and the other three genera belong in group II. The secondary xylem of the genera of group II are similar in all aspects except for the size of the intervacular pitting. *Prockia* differs from these genera in that it has long radial multiples and/or radial pore chains, no spiral thickenings in the vessels, no perforated ray cells, exclusively simple perforation plates, and small vessel pitting (group VI). Other features such as ray height and width and crystal type and arrangement tend to unite *Prockia* with the other genera of tribe Prockieae; however, the woods of *Prockia*, *Banara*, *Scolopia*, and *Homalium* are so similar that it is difficult to distinguish among some species of these genera. Although the secondary xylem of *Prockia* suggests a close alliance with the Scolopieae, Banareae, and Homalieae, *Prockia* and the other genera of the Prockieae are united florally by their common possession of axile placentation. Thus, *Prockia* should remain united with the other genera of the Prockieae.

Gilg (1925) placed the genera of the Prockieae in subtribe Prockiinae of tribe Scolopieae (including the Banareae). The wood anatomy can support Gilg's arrangement since all the genera of the Prockieae are grouped together in the subtribe Prockiinae and a relationship to the genera *Scolopia* and *Banara* is implied by the inclusion of all these genera in the tribe Scolopieae.

The xylem anatomy could also support the placement of tribe Prockieae in the family Elaeocarpaceae. On the basis of the axile placentation and valvate calyx, Hutchinson (1967) established the tribe Prockieae in the

Tiliaceae (including the Elaeocarpaceae). For the same reasons, Bentham and Hooker (1862) included the known Prockieae as a separate tribe in their Series B Heteropetalae, a taxon equivalent to the Elaeocarpaceae. A comparison of Kukachka and Rees' (1943) description of the xylem anatomy of Tiliaceae and Elaeocarpaceae with the secondary xylem of tribe Prockieae suggests a close alliance between tribe Prockieae and the Elaeocarpaceae.

Keating (1973) notes that the Scolopieae, Banareae, Homalieae, Flacourtieae, and Prockieae all have similar pollen morphology. He also notes a similarity between the pollen of tribe Homalieae (and presumably the Prockieae) and the family Elaeocarpaceae.

The evidence from pollen morphology and wood anatomy appears then to suggest that tribe Prockieae is closely allied to both the Flacourtiaceae and the Elaeocarpaceae. Thus the correct placement of the Prockieae is still somewhat in doubt.

Evidence from the wood structure also reveals a reduction series in the Prockieae. The intervacular pits are large (10–14 μm .) in *Macrohaseltia*, medium-sized (8–10 μm .) in *Pleuranthodendron*, and small (4–7 μm .) in *Hasseltia*. In addition, the vessel-ray pitting is coarse (over 10 μm .) in these three genera, but *Prockia* has vessel-ray and intervacular pits that are not only the same size but also small (4–7 μm .). Since *Prockia* has exclusively simple perforation plates and the other three genera have both simple and scalariform perforation plates, *Prockia* appears to be the most specialized of these four genera. Thus, a reduction in the size of the vessel pitting from *Macrohaseltia* to *Prockia* seems plausible. Whether there are any evolutionary trends related to this reduction series, however, cannot be determined at this time.

Tribe Flacourtieae. The xylem anatomy in the Flacourtieae (excluding *Aphloia*) is rather diverse. The anatomical groups represented in the tribe are as follows: group II — *Bennettiodendron*, *Azara* (rarely group I), *Carrierea*, and *Olmediella*; group III — *Poliothyrsis*, *Itoa*, and *Idesia* (rarely group II); group V — *Dovyalis*; group VI — *Xylosma* and *Flacourtia* (rarely group V). It is apparent that two groups of genera are present in the Flacourtieae. One group has large vessel pitting and the other group has small vessel pitting. These two groups are rather distinct and except for characters present in most genera of the Flacourtiaceae, the only feature which these two groups have in common is the presence of integumented prismatic crystals usually more abundant in the upright ray cells than in the ray cells of the multiseriate portion of the ray.

The seven genera with large vessel pits can be separated into two groups based on the size of the intervacular pits. One group has intervacular pits over 10 μm . in diameter and the other group has some intervacular pits under 10 μm . in diameter. The four genera with intervacular pits over 10 μm . do not have prismatic crystals in chambered ray cells and some of their fibrous elements are nonseptate. Of these genera, *Carrierea* and *Olmediella* have coarse spiral thickenings throughout the

vessels (FIGURES 16, 18). This seems to indicate that these two genera are more closely allied to each other than to *Idesia* and *Itoa*. The three genera with large vessel pitting and some intervacular pits under 10 μm . have septate fibrous elements. Thus, based on the wood structure, *Poliothyrsis*, *Bennettiodendron*, and *Azara* appear to be more closely related to each other than to the other four genera with large vessel pitting.

Of the four genera with small vessel pits, only *Dovyalis* has a slightly different wood structure. *Dovyalis* lacks spiral thickenings in the vessels and also does not have prismatic crystals in chambered upright ray cells.

Recently, Sleumer (1972a) stated that *Ludia* is morphologically very similar to *Scolopia* (tribe Scolopieae). As might be expected, this morphological similarity extends into the secondary xylem. In addition, species of *Ludia*, *Flacourtia*, and *Xylosma* of the Flacourtiaceae, *Scolopia* and *Bartholomaea* of the Scolopieae, *Homalium* and *Calantica* of the Homalieae, *Banara*, *Pineda*, and *Trimeria* of the Banareae, and *Prockia* of the Prockieae (Tiliaceae), as previously mentioned, are for the most part indistinguishable anatomically (APPENDIX I). Keating (1973) has found that the pollen morphologies of these genera are also scarcely distinguishable from each other.

Tribe Casearieae. For the most part, the wood structure of tribe Casearieae is homogeneous (APPENDIX I). *Tetrathylacium* and *Neoptychocarpus* are exceptions to this homogeneous structure.

Tetrathylacium is the only genus in Casearieae which has exclusively scalariform perforation plates and large vessel pitting (group I). The floral morphology of *Tetrathylacium* is similar to that of other genera in the Casearieae, and its position in the tribe has not been questioned by taxonomists. Although the structure of the wood is primitive, *Tetrathylacium* has a specialized floral structure. Apparently, *Tetrathylacium* has retained some primitive features of the xylem while the floral morphology evolved. Thus, the xylem anatomy of *Tetrathylacium* suggests that the forebears of the genera of Casearieae evolved from some ancient group which had exclusively scalariform perforation plates and large vessel pits (i.e. genera of group I). The data in APPENDIX I suggest that the tribe Berberidopsideae contains the ancestral stock of the Casearieae. This proposed line of evolution also agrees with the phylogenetic sequences of Warburg (1894) and Gilg (1925) (FIGURE 1).

Neoptychocarpus is the only genus in the Flacourtiaceae which has exclusively scalariform perforation plates and small vessel pitting (group IV); otherwise, the secondary xylem is similar to that of other genera of Casearieae (APPENDIX I). On the other hand, the intervacular pitting sometimes tends to be opposite, although it is not clear whether the pits are opposite because of genetic influences or opposite through crowding. Monachino (1948), however, considered that *Neoptychocarpus* was unquestionably correctly placed in the Flacourtiaceae. Whether the presence of exclusively scalariform perforation plates is the retention of a primitive flacourtiaceous feature or whether features of *Neoptychocarpus*

and the other genera of Casearieae are similar because of convergent or parallel evolution is difficult to ascertain.

If *Neoptychocarpus* belongs in the Casearieae, then it probably evolved along the same lines as *Tetrathylacium*. Like *Tetrathylacium*, *Neoptychocarpus* has retained the primitive scalariform perforation plates which are typical of the Berberidopsidae. However, in contrast to *Tetrathylacium*, *Neoptychocarpus* developed small vessel pitting.

Another possible line of evolution is through the genus *Lacistema* (Lacistemaceae). Assuming that opposite intervascular pits in *Neoptychocarpus* are opposite because of genetic influence and not because of some physical or mechanical adjustments, then the secondary xylem of *Lacistema* is similar to that of *Neoptychocarpus*. On the basis of floral morphology, Chirtoiu (1918) suggested that *Lacistema* is more closely related to the Flacourtiaceae than to any other family. Krause (1925) specifically suggested *Prockia* (Flacourtiaceae) as the closest genus to *Lacistema*. Hutchinson (1967) implied some relationship, since he placed the Lacistemaceae and Flacourtiaceae in the order Bixales. Although the floral structure of *Neoptychocarpus* is not closely similar to that of *Lacistema*, the wood anatomy does imply an alliance. However, until more evidence is found to support a closer relationship between *Neoptychocarpus* and *Lacistema*, *Neoptychocarpus* should remain in the Casearieae.

As mentioned before, *Hydnocarpus* and *Neoptychocarpus* have similar pollen, representing a rare type in the Flacourtiaceae (Schaeffer 1972). The similarity in secondary xylem between these two genera is no greater, however, than that between *Neoptychocarpus* and any other genus belonging to group I (APPENDIX I). *Neoptychocarpus* has small vessel pitting and integumented prismatic crystals, whereas *Hydnocarpus* has large vessel pitting and nonintegumented prismatic crystals. Also, *Hydnocarpus* has spiral thickenings in the vessel-element tails of some species and vitreous silica in the vessels of most species. Perhaps *Hydnocarpus*, as well as *Lacistema*, is closely allied to *Neoptychocarpus*; however, these relationships are not clear.

Anomalous Genera

Paropsia, *Barteria*, and *Ancistrothyrsus* (Passifloraceae). Hutchinson (1967), Sleumer (1970), and others consider the tribe Paropsieae of Gilg's Flacourtiaceae as a member of the Passifloraceae. In their study of the systematic anatomy of the Passifloraceae, Ayensu and Stern (1964) concluded that *Paropsia* and related genera are anatomically more similar to Passifloraceae than to Flacourtiaceae. The wood structure of *Paropsia*, *Barteria*, and *Ancistrothyrsus*, differs greatly from that in the Flacourtiaceae. With anatomical evidence and with corroborating observations presented by Ayensu and Stern (1964), Den Berger (1928), Tupper (1934), Sleumer (1970), De Wilde (1971), and Hutchinson (1967), I concur that *Paropsia*, *Barteria*, and *Ancistrothyrsus* are members of the Passifloraceae and not of the Flacourtiaceae.

Soyauxia (Passifloraceae? Medusandraceae?). *Soyauxia* of Gilg's Paropsieae seems out of place in either the Passifloraceae or the Flacourtiaceae. The features of *Soyauxia* (APPENDIX I) suggest a relationship with a primitive group of plants, but probably not the primitive *Berberidopsis* and *Streptothamnus* of the Flacourtiaceae; at least no close relationship is evident. *Soyauxia*, *Berberidopsis*, and *Streptothamnus* have some features in common, such as solitary pores, long vessel and tracheid elements, and exclusively scalariform perforation plates; however, the structure of the rays and the axial parenchyma differs in each genus. *Soyauxia* has uniseriate rays and an abundance of parenchyma and silica in the ray cells, whereas *Berberidopsis* and *Streptothamnus* have large rays and lack axial parenchyma and silica.

On the basis of a central column in the ovary, Brenan (1953) placed *Soyauxia* in Medusandraceae. Studying the anatomy of *Soyauxia*, Metcalfe (1962) stated, ". . . although there are points of similarity in the structure of these two genera, *Medusandra* differs from *Soyauxia* in possessing a well developed system of secretory canals." Metcalfe argued that this anatomical difference together with morphological differences supports the view that *Soyauxia* and *Medusandra* are not closely related. Using the anatomy of *Peridiscus* (Peridiscaceae) as supporting evidence, Metcalfe also contended that *Soyauxia* is more closely allied to the Flacourtiaceae than to the Passifloraceae. The xylem anatomy does not suggest the placement of *Soyauxia* in the Flacourtiaceae, Passifloraceae, or Peridiscaceae, and until more evidence is available, the placement of *Soyauxia* must remain uncertain.

Peridiscus (Peridiscaceae). Both Warburg (1894) and Gilg (1925) indicated that *Peridiscus* is questionably a member of the Flacourtiaceae. In 1959, Hutchinson accepted the Peridiscaceae and placed it in his Tiliales. Later, in 1967, Hutchinson placed the Peridiscaceae in his Bixales and near the Flacourtiaceae. Sandwith (1962) added the genus *Whittonia* to the Peridiscaceae, and in a sequel to his paper, Metcalfe (1962) discussed the systematic anatomy of the Peridiscaceae. Metcalfe concluded that, "Peridiscaceae may quite well be allied to the Flacourtiaceae." In some respects the wood anatomy of *Peridiscus* is similar to that of some primitive genera of Flacourtiaceae, such as *Erythrospermum*. Both these genera have exclusively scalariform perforation plates, opposite intervascular pitting, and large vessel pitting. In addition, the ray structure, fiber length to vessel length ratio, and vessel and fibrous-element length are similar (APPENDIX I). The major differences between *Peridiscus* and most Flacourtiaceae are the absence of prismatic crystals, the presence of many nonseptate fibrous elements, and the abundance of either diffuse or reticulate (in short tangential lines) apotracheal parenchyma. Therefore, I agree with Metcalfe (1962), who believes that *Peridiscus* is definitely not a member of the Flacourtiaceae; yet the secondary xylem does suggest that *Peridiscus* is allied to the family.

Aphloia (= *Neumannia*, Neumanniaceae). Although the floral morphol-

ogy is somewhat specialized, *Aphloia* shows a primitive xylem anatomy. Hutchinson (1967) placed *Aphloia* in the tribe Flacourtiaceae. Under the name *Neumannia*, Warburg (1894) and Gilg (1925) also placed *Aphloia* in the Flacourtiaceae. According to Willis (1966), Van Tieghem proposed *Neumannia* as the basis of the monotypic family Neumanniaceae, which showed uncertain affinities to the Flacourtiaceae. The woods of *Aphloia* and the primitive genera *Berberidopsis* and *Streptothamnus* are similar.

In APPENDIX I the anatomy of these genera can be compared. For the most part, the floral morphology of *Aphloia* seems to resemble the genera of tribe Flacourtiaceae. However, Willis (1966) notes that there is "perhaps some justification for maintaining the family Neumanniaceae distinct." It is possible that *Aphloia* retained the primitive wood structure of the ancestral stock of tribe Flacourtiaceae while the floral structure evolved along the same line as the other genera of the Flacourtiaceae. However, I believe that *Aphloia* evolved from the same forebears as the genera of the Flacourtiaceae, but deviated sufficiently from the evolutionary line of the Flacourtiaceae to produce a combination of characters which could justify consideration of placement in a separate family.

Asteropeia (Asteropeiaceae). Hutchinson (1967) included *Asteropeia* in his tribe Banareae, but most taxonomists assign this genus elsewhere, generally to the Theaceae. According to Willis (1966), Takhtajan proposed the monotypic family Asteropeiaceae, showing possible affinities with the Linaceae, Tetrameristaceae, or Flacourtiaceae. Based on the wood anatomy (APPENDIX I), *Asteropeia* is not a member of the Flacourtiaceae and there does not seem to be any indication of close affinities with this family. According to Record (1942), the wood of *Asteropeia* is not related to that of the Theaceae. Thus, it seems that Takhtajan's monotypic family Asteropeiaceae is the best position for *Asteropeia*, at least until more information is available to indicate its affinity elsewhere.

Goethalsia (Tiliaceae). The floral and wood structure of *Goethalsia* is not flacourtiaceous. Generally *Goethalsia* is placed in the Tiliaceae, but following the recommendation of Gleason (1934), Hutchinson (1967) placed *Goethalsia* in the tribe Pangieae (Flacourtiaceae). In 1934, Record stated that ". . . the pith, bark and wood of *Goethalsia* all suggest Tiliaceae and not Flacourtiaceae." Burret (1934), a specialist in Tiliaceae, agreed with Record (1934) and noted that Gleason (1934) misinterpreted the flower structure of *Goethalsia*. When Kukachka and Rees (1943) studied the wood anatomy of the Tiliaceae, they found no evidence to support Gleason's transfer of *Goethalsia* to the Flacourtiaceae. Features found in *Goethalsia* and not in genera of the Flacourtiaceae include an abundance of axial parenchyma and nonseptate fibrous elements. Thus, I concur with Record (1934), Burret (1934), and Kukachka and Rees (1943) that *Goethalsia* is tiliaceous, not flacourtiaceous.

Triphyophyllum (Dioncophyllaceae). The xylem anatomy of *Triphyophyllum* (APPENDIX I) is definitely unusual for Flacourtiaceae. Hutchinson

(1967) submerged *Triphyphyllum* in *Dioncophyllum* and placed it in the tribe Scolopieae. Both Warburg (1894) and Gilg (1925) also included *Dioncophyllum* in their Scolopieae. In 1952, Airy Shaw proposed the family Dioncophyllaceae. He stated that "*Dioncophyllum* had nothing whatever to do with the Flacourtiaceae." In an anatomical study, Metcalfe (1952) supported Airy Shaw and suggested that ". . . there may well be affinities between the Dioncophyllaceae and the Nepentha-ceae and between the Dioncophyllaceae and Droseraceae." From personal observation, the wood anatomy supports the assertions of both Airy Shaw (1952) and Metcalfe (1952).

Lethedon (Thymelaeaceae or Aquilariaceae). Warburg (1894) placed *Lethedon* (= *Microsemma*) in a questionable group of Flacourtiaceae. Gilg (1925) excluded *Lethedon* from the Flacourtiaceae and placed it in the Thymelaeaceae. Hutchinson (1967) placed *Lethedon* in the Aquilariaceae, a segregate of Gilg's Thymelaeaceae. The secondary xylem of *Lethedon* (APPENDIX I) is definitely not flacourtiaceous, and from the morphology it seems likely that *Lethedon* is related to the Thymelaeaceae or Aquilariaceae.

FAMILY RELATIONSHIPS

Ancestral stock. Judging from the primitive wood structure in some branches of the extant Flacourtiaceae, immediate progenitors of the plants we recognize today as Flacourtiaceae must have been relatively unspecialized. According to Hutchinson (1967), the family Flacourtiaceae is a somewhat indeterminate and intermediate group of plants, somewhere between the Dilleniaceae (Dilleniales) and the order Tiliales. Takhtajan (1969) also suggests a Dilleniacean ancestry, but Cronquist (1968) proposes a Thealian one.

Many characters in the Dilleniaceae and in the two primitive genera of Flacourtiaceae are parallel. Features of the wood which occur in the Dilleniaceae but do not appear in *Berberidopsis* and *Streptothamnus* include larger and fewer pores, more axial parenchyma, and raphide crystals. There are free carpels and distinct sepals and petals in the Dilleniaceae but not in *Berberidopsis* and *Streptothamnus*. The secondary xylem of the Dilleniaceae is also similar to that of the Theaceae, and Dickison (1967) suggests that the similarity of wood structure supports the taxonomic alliance between the Dilleniaceae and Theaceae. As might be expected, the woods of *Berberidopsis* and *Streptothamnus* resemble the woods of the Theaceae. Features not found in *Berberidopsis*, *Streptothamnus*, or the Dilleniaceae, but which do occur in the Theaceae, include shorter and narrower rays, a 3-5-locular ovary, scanty endosperm, and axile placentation. Since there appears to be more similarity among *Berberidopsis* and *Streptothamnus* and the Dilleniaceae, the ancestral stock of the Flacourtiaceae would appear to lie in the Dilleniaceae as opposed to the Theaceae.

Cronquist derives the family Flacourtiaceae (Violales) from the Theales and through a different line of evolution also derives the Elaeocarpaceae (Malvales) from the Theales. He notes a similarity between Flacourtiaceae and Elaeocarpaceae, but concludes that their similarity is a product of common ancestry. Because of similar secondary xylem and pollen morphology of the Flacourtiaceae and Elaeocarpaceae, I would expect a more direct line of evolution from the Dilleniales through the Flacourtiaceae to the Tiliales or Malvales, as proposed by Takhtajan (1969) and Hutchinson (1967).

Additional evidence supporting the evolution of the Tiliales or Malvales from the Flacourtiaceae is shown in data from chemotaxonomy. According to Alston and Turner (1963), certain Malvales, especially Sterculiaceae, contain the fatty acid, sterculic acid, which has a three-membered ring. In some Flacourtiaceae, fatty acids with five-membered rings (chaulmoogric and hydnocarpic) are present. Fatty acids with ring structures are not only rare in the plant world, they are also very specific for genera, families, and possibly even for orders. It is easy to imagine then that plants producing cyclic fatty acids with a three-membered ring could have evolved directly from taxa having fatty acids with a five-membered ring.

Intraordinal relationships. The xylem anatomy cannot negate the supposed alliance among the families generally placed in the same order as the Flacourtiaceae. Williams (1962) and Keating (1968) studied the comparative morphology of the Bixaceae and Cochlospermaceae respectively. They found that these two families are more closely related to each other than to any other family. Comparing the Cochlospermaceae and Flacourtiaceae, Keating states, "further, Flacourtiaceae . . . better overlap the range found in Cochlospermaceae than in any other parietalian families named." In a subsequent paper, Keating (1973) noted that the pollen of both the Bixaceae and the Cochlospermaceae lies within the range of the Flacourtiaceae. My work also supports Keating's findings.

Another family similar to the Bixaceae and Cochlospermaceae is the Cistaceae. The anatomy of these small families resembles that of somewhat selected groups of Flacourtiaceae. In addition, the Flacourtiaceae is more primitive than any of these three families. Vestal (1937) proposed a phylogeny of these four families based primarily on wood anatomy. He concluded that the Flacourtiaceae gave rise to the Bixaceae and Cochlospermaceae and that the Bixaceae gave rise to the Cistaceae. This phylogenetic sequence cannot be negated from the evidence gathered from the secondary xylem, but neither can it be strongly substantiated or a close alliance established.

According to Metcalfe and Chalk (1950) and Taylor (1938, 1972), the wood anatomy in the Violaceae is similar to that in the Flacourtiaceae. Taylor (1972) contends that anatomical information ". . . reinforces the suggestion of kinship between the Violaceae and Flacourtiaceae." Takhtajan (1969) states that the family Violaceae is closely allied to the Fla-

courtiaceae through the primitive tribe Rinoreae (Violaceae). Hutchinson (1969) places the Violaceae in its own monotypic order somewhat distant from the Flacourtiaceae and the rest of the Bixales. The anatomical resemblance, coupled with taxonomic evidence, seems to outweigh Hutchinson's arguments for placing the Violaceae in an order by itself.

The relationship of the Peridiscaceae and Lacistemaceae has previously been discussed. The xylem anatomy of *Peridiscus* (Peridiscaceae) indicates a close alliance to the primitive taxa of Flacourtiaceae. *Neoptychocarpus*, of the tribe Casearieae (Flacourtiaceae), and *Lacistema* (Lacistemaceae) have similar wood structure. In addition, the pollen morphology also supports a close alliance (Keating 1973).

Order Passiflorales. According to Hutchinson (1969), ". . . Passiflorales, . . . probably derived from Bixales, show close relationships with Flacourtiaceae." In addition, Takhtajan (1969) states that "it is very difficult to draw a clear taxonomic boundary between the two most primitive families — Passifloraceae and Flacourtiaceae." Species of *Passiflora* (Passifloraceae) and *Hydnocarpus* and *Rawsonia* (Flacourtiaceae) show a positive reaction to antifungal activity tests (Nicolls 1970). The chemical causing antifungal activity is not known, but it is thought to be the same in both the Flacourtiaceae and Passifloraceae, thus supporting a close family relationship. The secondary xylem of each of these families has many distinguishing features and they are easily separated anatomically. Although differences exist, in no way does the wood anatomy negate the possibility that the Passifloraceae is derived from the Flacourtiaceae.

Order Euphorbiales. The secondary xylem of the Euphorbiaceae (Euphorbiales) is diverse, and some selected genera of the Euphorbiaceae are very similar to selected genera of the Flacourtiaceae. Cronquist (1968) places the order Euphorbiales in his subclass V, Rosidae, which is phylogenetically distant from the Flacourtiaceae (subclass IV, Dilleniidae). Takhtajan (1969), Hutchinson (1967), and Sleumer (1954) all suggest somewhat of an alliance between the Euphorbiaceae and Flacourtiaceae. Takhtajan aligns the Euphorbiales close to the Malvales. He states that "one may therefore presume that the Euphorbiales arose from some ancient group intermediate between the Flacourtiaceae and Malvales."

Hutchinson (1967) and Sleumer (1954) point out the resemblance of some Flacourtiaceae, particularly those with unisexual flowers and no petals, to some genera of Euphorbiaceae. Hutchinson proposes that "perhaps a small part of Euphorbiaceae has arisen from the same stock as the Flacourtiaceae"; he also cites *Kiggelaria* (Flacourtiaceae) as a genus possessing characters of a few Euphorbiaceae. According to Metcalfe and Chalk (1950), the wood of *Antidesma*, *Bischoffia*, and *Phyllanthus* of the Euphorbiaceae is very similar to the wood of *Caloncoba*, *Erythrospermum*, and *Kiggelaria* of the Flacourtiaceae. Furthermore, the genera *Acalypha*, *Aporosella*, *Glochidion*, and *Hymenocardia* of the Euphorbiaceae suggest an alliance with the genera of the tribes Casearieae, Homalieae, and Flacourtiaceae (in part). These morphological and anatomical similarities

may be due to convergent evolution, as envisioned by Cronquist (1968); however, since a moderate number of both morphological and anatomical similarities are noted, it seems probable that some Euphorbiaceae and some Flacourtiaceae are allied, if not directly, then through common ancestry.

Order Salicales. According to Takhtajan (1969) and Cronquist (1968), the Salicales is derived from the Violales (including the Flacourtiaceae). Generally, this order is thought to be isolated and not closely related to any particular group, although it is often associated with taxa of the "Amentiferae." Hutchinson (1969) derived the Salicales from the Hamamelidales; however, Takhtajan and Cronquist claim that the gynoecium of Salicales is anomalous to that found in the subclass Hamamelidae. In an investigation of nectary structure, similarities were noted between the Violales and Salicales. In addition, similarities exist between pollen of some Flacourtiaceae and Salicaceae, although the pollen of Salicaceae is also similar to that of other unrelated families (Cronquist 1968; Keating 1973). However, investigations of the secondary phloem, chemistry, and hair structure suggests that the Flacourtiaceae and Salicaceae are not allied (Metcalf & Chalk 1950).

According to Takhtajan (1969), who cited an unpublished thesis by Gzyrian (1952) which I did not see, the wood anatomy of Salicaceae is closer to the wood anatomy of Flacourtiaceae than to that of any other family. Takhtajan states that "both in external morphology and in wood anatomy the greatest similarity to the Salicaceae is observed in the subtribe Idesiinae of the Flacourtiaceae." If the wood of *Salix* and *Populus* (Salicaceae) and *Idesia* and *Itoa* (Idesiinae, Flacourtiaceae) are compared, many similarities, such as intervacular and vessel-ray pitting, type of perforation plate, and absence of axial parenchyma, are found to exist among these genera. In the Salicaceae, the more obvious differences include shorter and narrower rays, homocellular or heterocellular rays with only a few rows of upright cells, and no prismatic crystals or septate fibrous elements. Although these differences are distinct, the xylem anatomy does not reveal any features which would negate the evolution of the Salicaceae from Flacourtiaceae.

In addition, it is possible to construct a reduction series from *Idesia* and *Itoa* to *Populus* and *Salix*. The rays of *Idesia* and *Itoa* are 2- to 4-seriate and heterocellular with long uniseriate extensions. A reduction in the width of the rays and in the number of rows of upright ray cells, coupled with the complete loss of septate fibrous elements and prismatic crystals, would produce a wood structure resembling that of *Salix*. With the elimination of upright ray cells in *Salix*, secondary xylem resembling that of *Populus* would be evident. Carlquist's (1961) trends in the evolution of ray types in dicotyledons would support this possibility.

Stern and Brizicky (1958) have pointed out that it is necessary to be aware of the potentially erroneous conclusions inherent in selecting genera from a large heterogeneous family, such as the Flacourtiaceae, for

comparison with homogeneous families of a few genera. However, I believe that enough evidence has been gathered from the floral and wood structure to favor the evolution of the Salicales from Violaes (including the Flacourtiaceae). Conclusive evidence supporting or negating this evolutionary trend must come from other independent fields of inquiry.

Orders Tamaricales and Capparales. Since the woods of Tamaricaceae and Capparaceae are relatively specialized and the woods of Flacourtiaceae are more primitive, the xylem anatomy cannot negate the possibility that Tamaricaceae (Tamaricales) and Capparaceae (Capparales) are derived from Flacourtiaceae (Violaes or Bixales), but the numerous dissimilarities in the secondary xylem do not support such a derivation.

SUMMARY AND CONCLUSIONS

Anatomically, the Flacourtiaceae is composed of homogeneous tribes loosely united into a family. Based on the types of perforation plates and vessel pits, six anatomical groups are defined. The phylogeny of these groups is determined assuming a monophyletic origin for the Flacourtiaceae. Small vessel pitting in Flacourtiaceae is apparently a more specialized feature than large vessel pitting. In comparing the phylogeny of tribes of Flacourtiaceae, as proposed by Warburg and Gilg, to the phylogeny of the anatomical groups, a strong correlation is suggested. In addition, the wood anatomy supports Hutchinson's definition of the tribes Berberidopsidae and Oncobeeae formerly included in Gilg's tribe Oncobeeae.

For the most part, the wood anatomy supports the generic and tribal composition of Hutchinson's Flacourtiaceae. The transfer of Gilg's tribe Paropsieae from Flacourtiaceae to Passifloraceae is confirmed. On the basis of axile placentation and valvate calyx, Hutchinson transfers Gilg's subtribe Prockiinae (tribe Scolopieae) from the Flacourtiaceae to the tribe Prockieae in the Tiliaceae (including the Elaeocarpaceae). The secondary xylem in genera of tribe Prockieae is flacourtiaceous; however, the wood anatomy in the Prockieae is similar to that in the Elaeocarpaceae. Consequently, if tribe Prockieae is to be transferred on a morphologic-taxonomic basis, the evidence from the wood anatomy endorses the placement of the Prockieae in the Elaeocarpaceae.

Berberidopsis and *Streptothamnus* have distinctive wood anatomy for Flacourtiaceae. They have very long tracheids, solitary pores, very long vessel elements, and scalariform perforation plates which suggest a very primitive condition. Perhaps a new family should be defined to contain these two aberrant genera.

Hydnocarpus apparently has retained some of the primitive xylem features of the common ancestral stock of the Pangieae and Oncobeeae. The long vessel and fibrous elements, opposite intervascular pitting, and scalariform perforation plates suggest the placement of *Hydnocarpus* in the primitive tribe Berberidopsidae, but the floral structure negates such a

suggestion. Chemotaxonomy indicates an alliance with the Oncobeeae since only species of *Hydnocarpus* and some genera in Oncobeeae contain chaulmoogra oil. In addition, the wood anatomy favors the submersion of *Taraktogenos* and *Asteriastigma* in *Hydnocarpus*.

The secondary xylem in the genera of the Scolopieae, Banareae, and Homalieae and in the genus *Prockia* of the Prockieae (Tiliaceae) is so similar that many genera among these tribes are not easily distinguishable anatomically. Thus, the xylem anatomy can neither support nor negate Hutchinson's formation of the new tribe Banareae and his transfer of *Trimeria* from tribe Homalieae to the Banareae. However, since *Prockia* is distinctive florally, it should remain united with the other genera of the Prockieae. In addition, a reduction series of vessel pitting is proposed for the genera of the Prockieae.

Tribe Flacourtieae has two major groups of genera, one of which has small vessel pitting and the other large vessel pitting. Furthermore, two subgroups exist within the group possessing large vessel pits.

Tetrathylacium and *Neoptychocarpus* of the specialized tribe Casearieae have exclusively scalariform perforation plates. Since *Tetrathylacium* has large vessel pitting (group I) and florally fits well in the Casearieae, it appears to have retained the primitive xylem structure from its ancestral stock, probably among the Berberidopsidae. In contrast, *Neoptychocarpus* has scalariform perforation plates and small vessel pitting; otherwise, it is similar to any other genus of the Casearieae. In many respects the secondary xylem of *Lacistema* (Lacistemaceae) is similar to that of *Neoptychocarpus*; thus, *Lacistema* and *Neoptychocarpus* might have evolved from the same forebears that gave rise to the Flacourtiaceae. However, more evidence is needed to support a close alliance between *Neoptychocarpus* and *Lacistema*.

Hutchinson's placement of the genera *Aphloia*, *Asteropeia*, *Dioncophyllum*, and *Goethalsia* in the Flacourtiaceae is negated on the basis of the xylem anatomy. *Aphloia* is anomalous as a member of the tribe Flacourtieae, for it has a primitive and unusual wood structure which to some extent resembles that of *Berberidopsis* and *Streptothamnus*. Therefore, the character of the xylem anatomy supports the proposed monotypic family Neumanniaceae, which has affinities with the Flacourtiaceae. The wood of *Asteropeia* is certainly not flacourtiaceous. Since Record (1942) and others rule out the Theaceae, the proposed monotypic Asteropeiaceae may be justified. Airy Shaw's (1952) statement that "*Dioncophyllum* [has] nothing whatever to do with the Flacourtiaceae" agrees with the evidence from the xylem. The secondary xylem and floral morphology suggest that *Goethalsia* is tiliaceous, not flacourtiaceous. Other genera sometimes associated with the Flacourtiaceae, but having nonflacourtiaceous wood structure, include *Peridiscus* (Peridiscaceae), *Soyauxia* (possibly Medusandraceae or Passifloraceae), and *Lethedon* (= *Microsemma*, Thymelaeaceae or Aquilariaceae).

The stock from which the Flacourtiaceae arose appears to be represented in the forebears of the Dilleniales. According to Cronquist, Fla-

courtiaceae (Violales) is derived from Dilleniales through the Theales. The secondary xylem of *Berberidopsis* and *Streptothamnus* is primitive and seems to indicate affinities with the Dilleniaceae. Thealean ray structure, axile placentae, and scanty endosperm are not suggestive of a flacourtiaceous ancestry.

The other families placed in the same order as Flacourtiaceae are for the most part more specialized than Flacourtiaceae. The wood anatomy does not negate any proposed intraordinal relationships; however, strong support for many of these relationships is also lacking. In some cases the wood structure of families in other orders is more similar to that of the Flacourtiaceae than the wood structure of families within the same order.

The xylem anatomy supports the derivation of order Passiflorales from the Flacourtiaceae through the tribe Paropsieae. Also, based upon anatomical structure, the Malvales or the Tiliales could be derived from the Flacourtiaceae through tribe Prockieae (Tiliaceae). In both cases chemotaxonomic evidence supports such derivations.

Selected genera of Flacourtiaceae and Euphorbiaceae have similar wood structure, lending support to the proposed evolution of order Euphorbiales from the Flacourtiaceae. *Idesia* and *Itoa* of the Flacourtiaceae and *Populus* and *Salix* of the Salicales have similar secondary xylem in some respects, and no features were found which would negate the evolution of order Salicales from the Flacourtiaceae. It has also been suggested that the Tamaricales and Capparales are derived from the Flacourtiaceae. Although the xylem anatomy does not negate the derivation of these orders from the Flacourtiaceae, support for such phylogenies is lacking.

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THE NEOTROPICAL GENUS TACHIA (GENTIANACEAE)

BASSETT MAGUIRE AND RICHARD E. WEAVER, JR.

THE GENUS *Tachia* Aublet, consisting of nine species as here recognized, is characteristic of the rain forest lowlands and midlands of the Hylaea. It is unusual among the genera of the Gentianaceae in that characters separating it from others are well marked and constant.

All species are semierbaceous or soft-stemmed perennials that usually develop a single stem. Sometimes they assume small treelike aspects. The essentially sessile flowers, arising in succession from a "cushion" or broad short shoot in the axils of the leaves, and the ovary mounted on a short, persistent, fibrous peg are unique in the family. Some species seem to be imperfectly delineated, possibly because of the scarcity of collected material. Such taxa here recognized may in the future, in the light of more adequate observation, require re-evaluation.

MORPHOLOGY — ANATOMY

Habit. As noted above, all members of the genus are perennial with subligneous, commonly subvirgate and little branched, quite characteristically greenish or bright yellow stems. This yellow coloration, present also in the calyces and often in the corollas, makes the plants conspicuous in their forest habitats.

Leaves. The leaves are entire and petiolate. Species of section TACHIA develop penniveined, coriaceous or chartaceous, seldom membranaceous blades. Those of section SCHOMBURGKIANA are invariably tri- or quintuple-veined and somewhat membranaceous.

Flowers. The calyx provides excellent and consistent criteria for the distinction of species in its degree of division, i.e., in the relative length of tube and lobes. The development or absence of calyx keels is consistent. In *Tachia schomburgkiana* the keel becomes a prominent wing which is extended and oriented beyond and at right angles to the plane of the calyx tube as a prominent lobe.

The corolla is tubular, often somewhat ventricose or expanded, with lobes commonly considerably shorter than the tube. In *Tachia parviflora* the tubes and lobes are essentially equal in length.

The five stamens are commonly exserted; their filiform filaments are adnate to the corolla tube, the point of attachment being a dependable character in the separation of species. Anthers are introrse, oblong, caudate and basifixed, with connective not produced, although the region of transition may sometimes be at an angle with the plane of the anther. Dehiscence is longitudinal and ventral.

The gynoecium is surmounted on a short but obvious glandular-lobed

gynobase, and is 2-carpellary. The ovary is unilocular, but the lateral sutures are deeply intruded, and placentation, therefore, is sometimes sub-pseudoaxillary. Styles exceed the ovary but are sometimes deciduous. The stigma is bilamellate.

Seeds are small, usually coarsely papillate, subprismatic, and commonly 0.4–0.6 mm. in longest axis.

Pollen. The pollen grains are sphaeroidal or rarely ellipsoidal, tricolporate, and usually 30–40 μm . along the longest axis. The exine is typically reticulate, but the width of the lumina, and therefore the coarseness of the reticulum, vary enormously from species to species. In *Tachia guianensis*, *T. grandifolia*, and *T. schomburgkiana* the lumina are large and the reticulum is relatively fine. In *T. parviflora*, however, the lumina are greatly reduced and the exine appears merely punctate. Finally, in *T. occidentalis* the exine appears completely smooth except for the presence of a few, irregularly spaced globules.

Unfortunately, as Nilsson (1967, 1968, 1970) has found to be the case with many Gentianaceae, the variation in pollen grain morphology is not correlated with gross morphological variation. Therefore, although it does provide specific characters, pollen morphology is of little phyletic significance in this genus.

PHYLOGENY AND GEOGRAPHY

Distribution patterns of the species of *Tachia* show a checkerboard configuration (MAP 1). From the material now available, no two species seem to be sympatric except *T. occidentalis* and *T. parviflora*, and these in only a small part of their assumed overlying ranges. For six species the ranges are, comparatively, "eastern" and local. Three species are "western": the range of *T. occidentalis* is the largest, albeit somewhat disjunct; that of *T. loretensis* is local; and that of *T. parviflora* is limited, but greatly disjunct.

There seems to be no significant geographic or ecologic correlation with presumptive systematic relationships within the genus. Indeed, if the members of section SCHOMBURGKIANA, so delimited largely because of the plinnerved leaves, are considered the more primitive group, then its members have achieved the more extended distribution, with the distinctive *Tachia schomburgkiana* occupying a compact range on the eastern periphery of the Roraima sandstone sediments of Guyana and contiguous Venezuela, and the disjunct *T. parviflora* a range of eastern middle altitudes in central Peru and of similar habitat in Amazonian Bolivia. The indefinite locality for the original collection of *T. gracilis*, and the scanty collections from the pediments of Cerro Marahuaca of Roraima sediments in Territorio Amazonas of Venezuela, offer remote intermediate geographic connection.

Distribution of the six members of section TACHIA, characterized by penniveined leaves, similarly does not present any persuasive indication of progressive distribution as related to morphologic modification.

Tachia would fit into the Tachiinae of the Gentianeae as ordered by



MAP 1. Distribution of species of *Tachia*.

Gilg (1895) and thus be aligned in our area with *Macrocarpaea* (Griseb.) Gilg and the later described *Chorisepalum* Gleason & Wodehouse, which is endemic to the Guayana Highland. Palynologically, *Tachia* is similar to these two genera.

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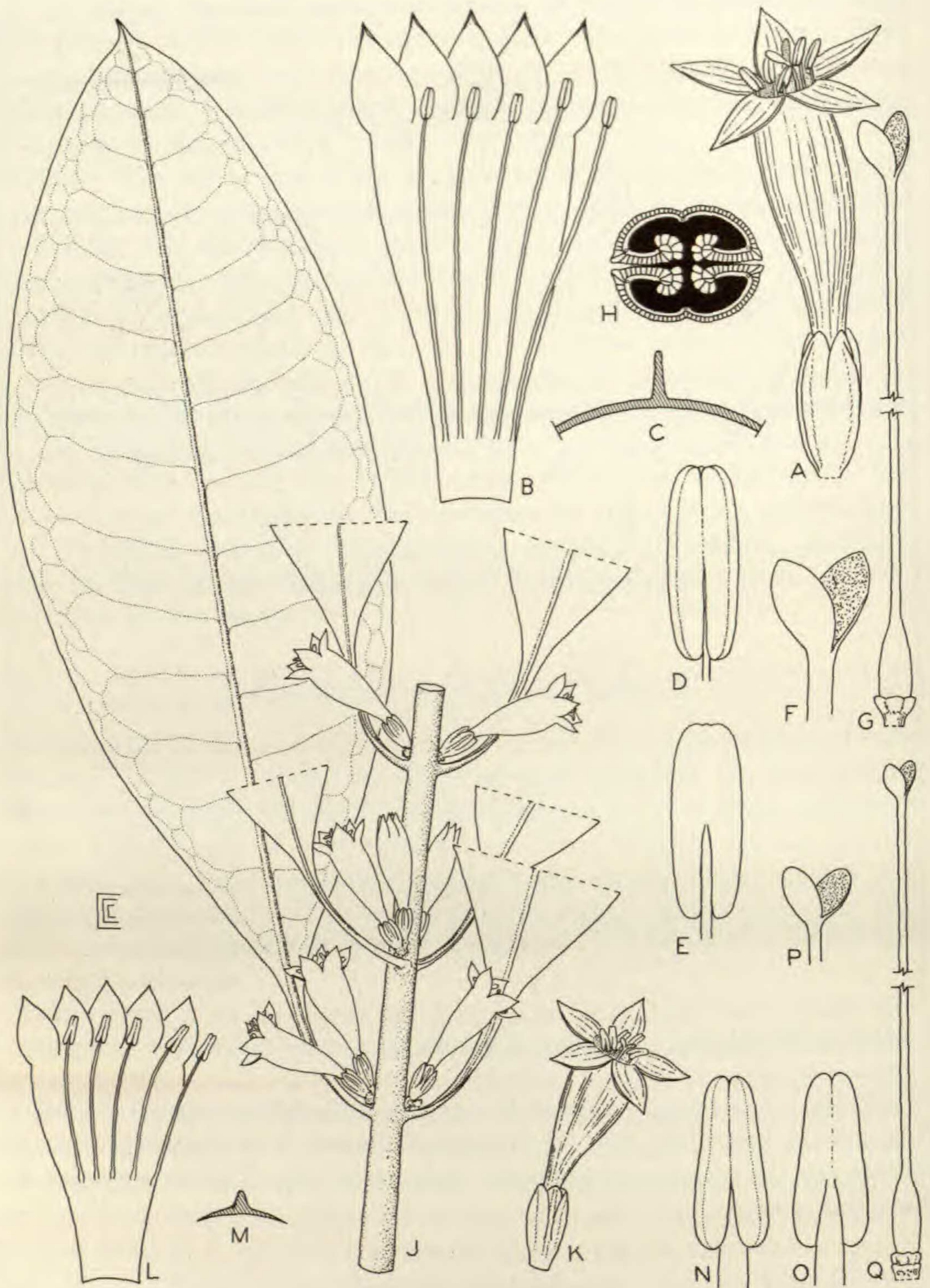


FIGURE 1. A-H, *Tachia occidentalis*. A, flower, $\times 1$; B, opened corolla, $\times 1$; C, sepal, cross-section diagram, $\times 6$; D, anther, ventral view, $\times 6$; E, anther, dorsal view, $\times 6$; F, stigma, *Schunke-Vigo 1047*, $\times 3$; G, pistil, *Schunke-Vigo 1047*, $\times 2$; H, capsule, cross-section diagram, *Wolfe 12229*. J-Q, *Tachia grandifolia*, all from *Silva & Brazão 60842*. J, habit, $\times 1/2$; K, flower, $\times 1$; L, opened flower, $\times 1$; M, sepal, cross-section, $\times 6$; N, anther, ventral view, $\times 6$; O, anther, dorsal view, $\times 6$; P, stigma, $\times 3$; Q, pistil, $\times 2$.

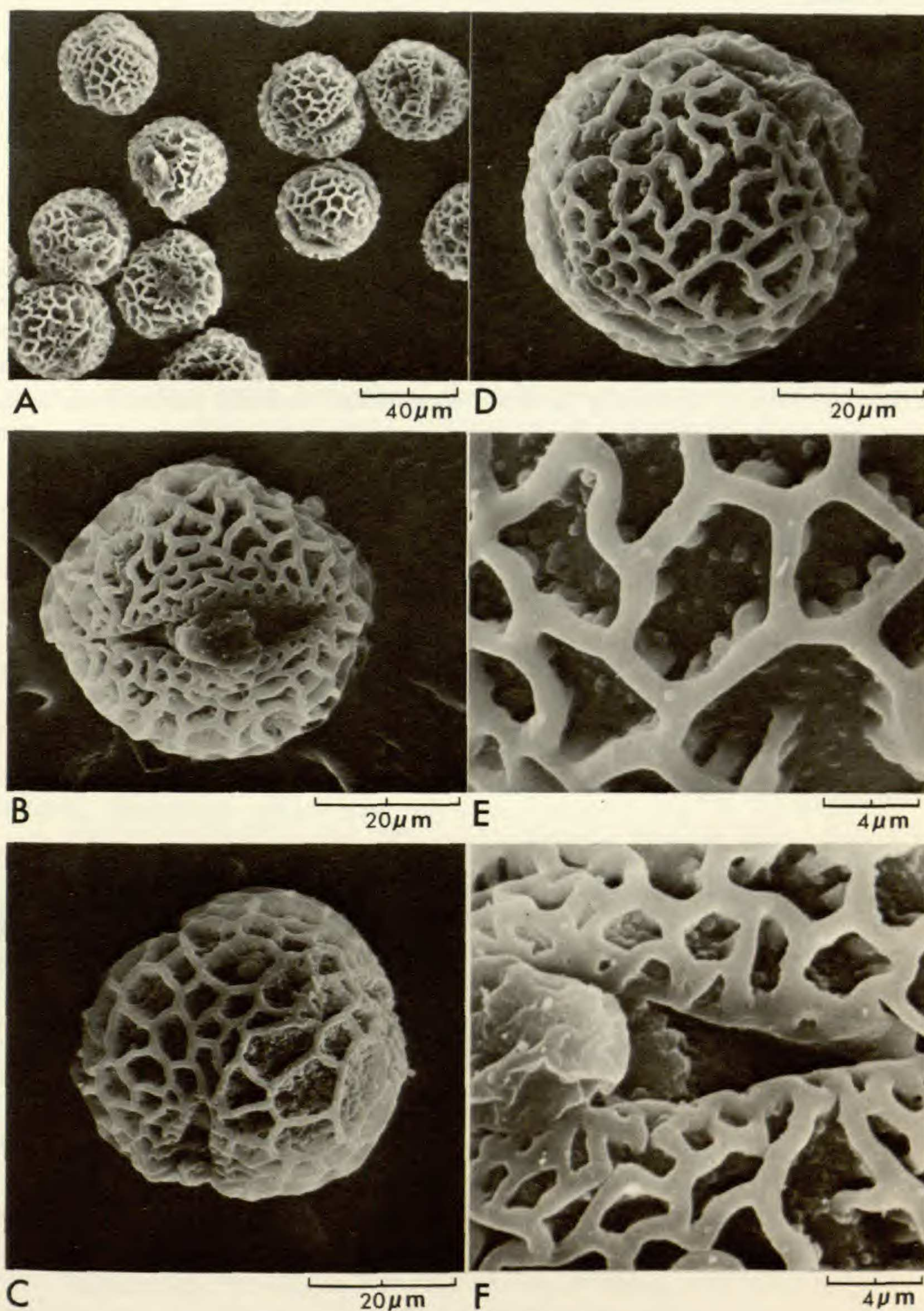


FIGURE 2. *Tachia grandifolia*, Maguire et al. 37496, SEM micrographs. Pollen grains sphaeroidal, 3-colporate, exine strongly reticulate. A, general field, $\times 500$; B, sulcus and pore, equatorial view, $\times 1500$; C, polar view, $\times 1500$; D, intersulci, equatorial view, $\times 1500$; E, reticulum, $\times 5000$; F, portion of pore and sulcus, $\times 5000$.

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SYSTEMATIC TREATMENT

Tachia Aublet, Pl. Guiane 1: 75. 1775.

Flowers 5-merous, solitary, rarely binary, sessile or subsessile on an axillary "cushion" or broad short shoot, thereupon often appearing seasonally and successively; calyx tubular, sometimes 5-carinate or alate, the lobes exceeding the tube or subequal, the interior at the base beset with a 5-lobed ring of upwardly directed squamellae; corolla infundibuliform, slightly ventricose, rarely short salverform, the tube much exceeding the apiculate lobes (except in *Tachia parviflora*); stamens 5, exserted, the filaments attached below the middle of the corolla tube or at the juncture of the tube and lobes, the anthers introrse, linear-oblong, caudate, basifixed, 4-celled; pollen grains simple, 3-colporate, sphaeroidal or rarely ellipsoidal, 33–45 μm . in diameter, the polar axis somewhat the longer, the exine clearly and sharply reticulate (psilate and globulate in *T. parviflora*), or punctate; the ovary borne on a short, persistent, glandular gynobase, 1-locular, the placentae deeply intruded, shortly inflexed, the ovules numerous; styles marcescent, exceeding the corolla; the stigmas strongly bilamellate; seeds numerous, small, prismatic, tuberculate.

Subligneous or soft-stemmed shrubby perennials, commonly simple-stemmed, often of small treelike aspect.

TYPE: *Tachia guianensis* Aublet.

This small genus may be divided into two groups, each reflecting close infrarelationships, one with pinnately veined leaves (6 species) and the other with quintuple-veined leaves (3 species). The most sharply distinctive species is *Tachia schomburgkiana*, with thin pli-veined leaves and a prominently winged calyx.

I. Section TACHIA. Blades of the leaves pinnately nerved.

Tachia guianensis (type species), *T. grandifolia*, *T. occidentalis*, *T. smithii*, *T. lorentensis*, and *T. grandiflora*.

II. Section Schomburgkiana Maguire & Weaver, sect. nov. Laminae foliorum quintuplinervatae.

Tachia schomburgkiana (type species), *T. gracilis*, *T. parviflora*.

KEY TO THE SPECIES OF TACHIA

A. Leaves inconspicuously penninerved (sect. TACHIA).

B. Calyx divided to below the middle; leaf blades thick and somewhat coriaceous, to 28 cm. long; corolla 4 cm. long or less; pollen grains sphaeroidal, exine reticulate. 1. *Tachia grandifolia*.